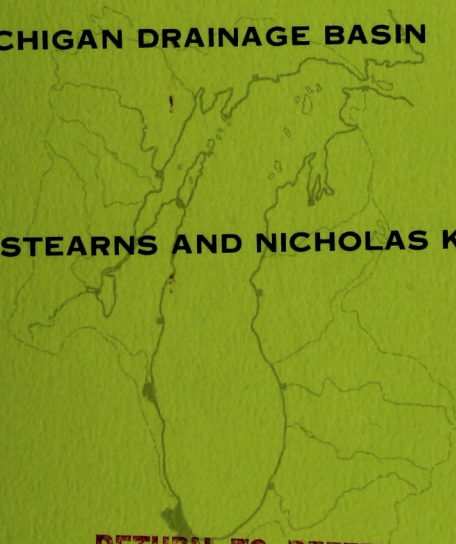# ENVIRONMENTAL STATUS OF THE LAKE MICHIGAN REGION

VOLUME 10. VEGETATION OF THE LAKE MICHIGAN DRAINAGE BASIN

FOREST STEARNS AND NICHOLAS KOBRIGER

U of C-AUA-USERDA

ARGONNE NATIONAL LABORATORY, ARGONNE, ILLINOIS

───────── NOTICE ─────────

ARGONNE NATIONAL LABORATORY
9700 South Cass Avenue
Argonne, Illinois 60439

ENVIRONMENTAL STATUS OF
THE LAKE MICHIGAN REGION

Volume 10. Vegetation of the Lake Michigan
Drainage Basin

by

Forest Stearns* and Nicholas Kobriger*

Consultants to
Environmental Statement Project

April 1975

*Department of Botany, University of Wisconsin--Milwaukee

CONTENTS

CONTENTS

FIGURES

TABLES

PREFACE

Assessments of the environmental impacts of individual nuclear power plants sited on the shores of Lake Michigan have led to increased recognition of the need for regional considerations of the environmental impacts of various human activities, and a compendium of information on the environmental status of the region for use in assessing such impacts. In response to these needs, a report series describing the status of Lake Michigan and its watershed is in preparation. The series is entitled "Environmental Status of the Lake Michigan Region"; this report is part of that series.

The report series provides a reasonably comprehensive descriptive review and analysis of natural features and characteristics, as well as past, present, and proposed natural processes and human activities, that influence the environmental conditions of Lake Michigan, its watershed, and certain adjacent metropolitan areas. This series will constitute a regional reference document useful both to scientific investigators and to other persons involved in environmental protection, resource planning, and management. In these regards, the "Environmental Status of the Lake Michigan Region" will serve in part as an adjunct to reports of broader scope, such as the Great Lakes Basin Commission's Framework Study.

Other Volumes Published to Date in this Series

Vol. 7. *Earthquake History and Measurement with Application to the Lake Michigan Drainage Basin.* Richard B. Keener. NTIS-$4.00. 19 pp.

Vol. 9. *Soils of the Lake Michigan Drainage Basin--An Overview.* Forest Stearns, Francis D. Hole, and Jeffrey Klopatek. NTIS-$4.00. 22 pp.

Vol. 15. *Mammals of the Lake Michigan Drainage Basin.* Charles A. Long. NTIS-$5.45. 109 pp.

ENVIRONMENTAL STATUS OF THE LAKE MICHIGAN REGION

VOL. 10.   VEGETATION OF THE LAKE MICHIGAN DRAINAGE BASIN

by

Forest Stearns and Nicholas Kobriger

Abstract

   *The presettlement vegetation of the Basin (described in Part 1)
consisted primarily of conifer, hardwood and mixed forests with
savanna grassland, shrub, dune, and sedge communities in the wet or
dry areas, reflecting the influences of postglacial climate, soil,
and disturbance. Settlers disturbed the vegetation by draining
wetlands and cutting the forests; extensive fires often followed
the logging. By 1920 most of the northern part of the Basin had
been logged. Crops and second-growth timber have replaced the
plants lost to the plow and ax (Part 2). Northern counties are now
reoccupied by northern mesic and xeric forest and aspen-birch
stands. With some exceptions, agriculture is confined to the
southern half of the Basin, wherein agricultural crops are the
dominant plant communities. Along the eastern shores in Michigan
and in Door County, Wisconsin, the moderating influence of Lake
Michigan permits extensive fruit production. Part 3 describes the
concept of plant succession and several routes by which it may
proceed, particularly primary succession on dunes and wetlands, and
secondary succession on logged or burned forest land, and old fields.*

PART 1.   NATURAL COMMUNITIES[*]

INTRODUCTION

   The modern history of the vegetation of the Lake Michigan Basin appears at
first glance relatively simple in contrast to many regions of North America.
Ice of the Wisconsin glacial period covered the entire Basin, overriding and
eliminating the forests and other communities that had existed in pre- and
interglacial times. As the ice retreated, it left a terrain covered by glacial
deposits, which differed in texture, chemical composition, and horizontal
layering. The postglacial history has been reviewed in detail in Wright and
Frey (1965).

---

[*]*L. Gysel, S. Stephenson and P. B. Whitford, consultants to the authors for
 Part 1.*

Despite the relatively short history of development, the vegetational pattern at the time of settlement was complex. Several factors operated to permit establishment of very different and yet stable communities in close proximity to each other. A youthful land surface, heterogeneity of soil, drainage, topography, climatic patterns, and disturbances by fire resulted in a complex pattern of native plant communities, each with its distinctive invertebrate, mammalian, and bird components. It is these communities that will be described in the following pages.

Deposition of glacial material produced a young topography, poorly drained, with a multitude of depressions, many of which became lakes. Postglacial drainage patterns have developed slowly, all the more so since many depressions were rapidly claimed by a variety of wetland plant communities and are now partially or entirely filled with peat or muck soils.

The climate of the Basin influenced postglacial invasion and establishment of the vegetation. After the ice disappeared, fluctuations in the postglacial climate between warm–dry and cool–moist periods resulted in oscillations of the prairie-forest border. Persistent drought conditions created a barrier restricting or preventing migration of tree species around the southern end of Lake Michigan; thus the major components of forest and wetland communities of eastern and northeastern Wisconsin may have reached there by migration around the northern tip of the lake. This climatic barrier may help to account for the present distribution of trees such as beech, now found along the western shore of Lake Michigan as far south as Milwaukee County, but which in the south penetrate westward only a few miles from the lake. However, other recent evidence suggests that a variety of vegetation may have existed during the Wisconsin glaciation in the driftless area of southwestern Wisconsin. This vegetation could easily have migrated northward and eastward. The restriction of northern mesic species to a band narrowing southward along the shore of Lake Michigan could have resulted from the postglacial warm–dry period of perhaps 4000 years B.C. which encouraged and maintained the invasion of prairie grassland into southeastern Wisconsin, northeastern Illinois, northern Indiana and, in patches, southwestern Michigan. Benninghoff (1964) suggested that the initial invasion of grassland into lower Michigan and Ohio may have occurred earlier, in a cool–dry period about 8000 years ago.

Reinvasion of plant communities along the eastern shore of Lake Michigan and throughout the Lower Peninsula of Michigan presumably resulted from north-ward and westward migration of mesic species from the beech-maple forest areas of central or southern Indiana and Ohio. This migration was preceded by a wave of coniferous forest (spruce-fir) that had persisted near the southern perimeter of the ice and moved northward during the slow retreat. At the time of European settlement, these northern species were common in conifer swamps as far south as northern Indiana.

During the glaciations, northern conifer communities were also present to the west in Minnesota (Wright, 1968), and they migrated eastward as those to the south moved northward.

In the longer time span, i.e., dating back to preglacial time, the plant components or flora of the Lake Michigan Basin came largely from Appalachian origins. The prairie or grassland community is an exception, since the component species are primarily of the plains; the refugia of the prairie during

the last glacial period lay to the west and south, in central and southern Illinois, Iowa, and Missouri.

In postglacial time, the American Indian played a role in maintaining some vegetational communities, although in large measure his activity merely supplemented natural events. Along the prairie border in Wisconsin, Illinois, Indiana, and, to a lesser extent, in Michigan, a combination of naturally and Indian-set fires maintained savanna vegetation, thus offering convenience in moving and hunting.

Indians may also have been responsible for major fires in the conifer forests, sometimes with catastrophic effects, but in these cases the Indians were as likely losers as instigators. The naturally set fires in the conifer forests resulted from a combination of drought and lightning, as is the case today in the western United States. The most frequent and intense fires occurred in those areas of pine growing on sandy soils and in pine or oak barrens commonly found on the driest sands. The extensive mature white pine forests found in Michigan and Wisconsin at the time of settlement might well have originated from catastrophic fires occurring in the early or mid-1500's (Stearns, 1950). Similar old stands of hemlock and white pine were found in Pennsylvania (Hough, 1943). Younger stands of red and white pine provided ample evidence of more recent and recurring fire.

Loucks (1970) suggested that, in the Lake States forests, repeated cycles of drought, fire, and regrowth have been responsible for maintaining a resilient mixture of forest communities, including aspen-birch and pine.

Across both Wisconsin and Michigan, the regional climatic gradient is reflected in the changing vegetation, whether native species, introduced weeds, or crops. Northern forest communities and plants become rare southward and tend to be found only in restricted habitats, while plants of southern forests or grasslands and the communities they form likewise disappear as one goes northward. However, one may recognize a transition zone in which there is an intermixture of northern and southern plant species (Curtis, 1959; Braun, 1950). This climatic, vegetational and soil transition is evident to the casual traveler, who observes the change from maple to pine forest and from corn to oats or pasture (Fig. 1).

The moderating effect of Lake Michigan influences the orientation of the tension zone across Wisconsin (Fig. 1). A cooler climatic regime, northern plants and plant communities, and northern soils are found southward along the lake shore for a considerable distance.

Midwestern universities have long been centers for the study of vegetation and much fine work has been done in each of the four states of the Lake Michigan Basin. Early studies were made by dedicated naturalists who were often practicing physicians. Later studies commissioned by the young states were concerned with agriculture or the forest resources.

Over the years a considerable mass of information has been accumulated, but only in Wisconsin was the work on vegetation drawn together in one comprehensive treatment. *The Vegetation of Wisconsin*, a description of regional vegetation unique in the United States for its depth and breadth of coverage,
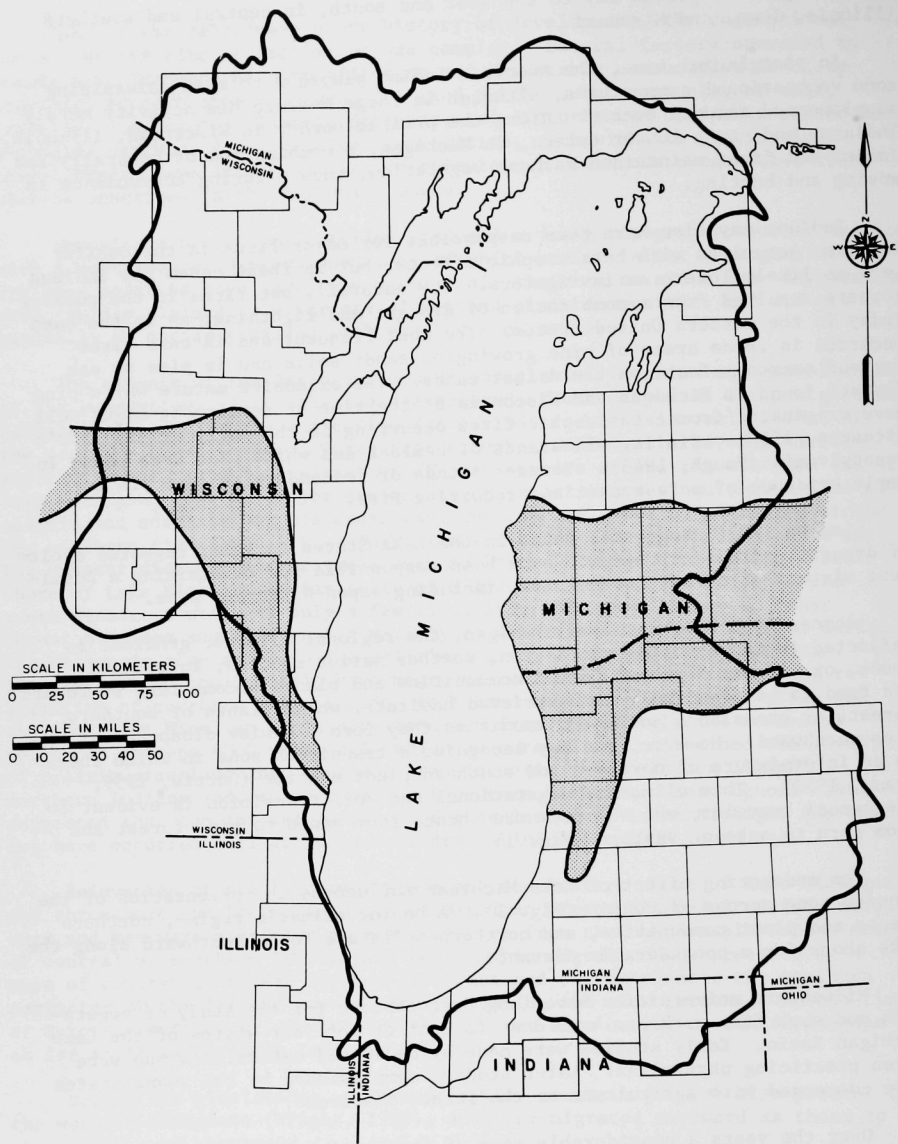
Fig. 1.   Vegetational Transition Zone ▓▓▓ in Michigan (Veatch, 1932) and
          Wisconsin (Curtis, 1959) and the Approximate Limit [- - -] of the
          Southern Mesic Forest (Braun, 1950).

was published by John Curtis in 1959. More recently, the Indiana Academy of Science (Lindsey, 1966) published a summary of the natural resources of Indiana in a book which reviews many vegetational studies. No comprehensive report is available for Michigan or Illinois. However, a number of studies are included in Braun's (1950) description of the deciduous forest. This section and those that follow will provide references to the regional summaries and to some of the specific and detailed studies which illuminate the nature, structure, and functioning of the major natural communities.

In Indiana, Michigan and Wisconsin, botanists, foresters and soil scientists have used the field notes of the General Land Office surveys to provide quantitative information on the nature and composition of vegetation during the early periods of settlement. These notes, carefully interpreted and supplemented by additional evidence, are the bases for maps of native vegetation. Others, working on particular aspects of regional vegetation, have mapped specific plant communities, groups of species, and individual species. A map of the prairie peninsula (Transeau, 1935) is especially pertinent since it documents the extensive eastward invasion of the grasslands during postglacial time.

Excellent maps exist for Wisconsin (Curtis, 1959), showing the original vegetation as delimited from early survey maps and additional sources. For Michigan, numerous county vegetation maps and a highly detailed state map have been published (Veatch, 1959). The Michigan maps are based on land survey data supplemented by soils information. Maps drawn for Indiana used these same types of data and other historical information (Lindsey, 1961). The Basin contains only a small portion of Illinois, and the Illinois communities in the Basin are essentially continuous with those of Wisconsin and Indiana. Vegetation maps of Illinois have also been prepared (Vestal, 1931; Anderson, 1970).

We have chosen to treat the various major native plant communities as separate describable entities and to indicate their general distribution and composition (Fig. 2). We prefer to offer the concept of a continuum of communities in summary, leaving the reader with the realization that intermediate types and intergradations do exist. Relationships between major communities north and south of the climatic tension zone are generalized in Figure 3.

The reader should also be aware that the relatively stable plant communities described in this section did not exist without change, but were found in a patchwork mosaic intermixed with transient and pioneer forests and wetlands which developed after disturbance and disappeared with normal successional process.

MICHIGAN
WISCONSIN

SCALE IN KILOMETERS
0 25 50 75 100

SCALE IN MILES
0 10 20 30 40 50

WISCONSIN
ILLINOIS

WISCONSIN

ILLINOIS

MICH.

OHIO

INDIANA

ILLINOIS
INDIANA

PRAIRIE AND SEDGE MEADOWS

OAK SAVANNA

SOUTHERN XERIC (OAK OR OAK-HICKORY) FOREST

SOUTHERN MESIC (MAPLE-BEECH) FOREST

SOUTHERN LOWLAND (HARDWOOD) FOREST

NORTHERN XERIC (PINE) FOREST AND PINE BARRENS

NORTHERN MESIC (NORTHERN HARDWOOD OR HARDWOOD-HEMLOCK) FOREST

NORTHERN LOWLAND (SWAMP CONIFER) FOREST

Fig. 2. Presettlement Vegetation of the Lake Michigan Drainage Basin.
Compiled from Veatch (1959), Lindsey (1961), Anderson (1970),
and Curtis (1959).
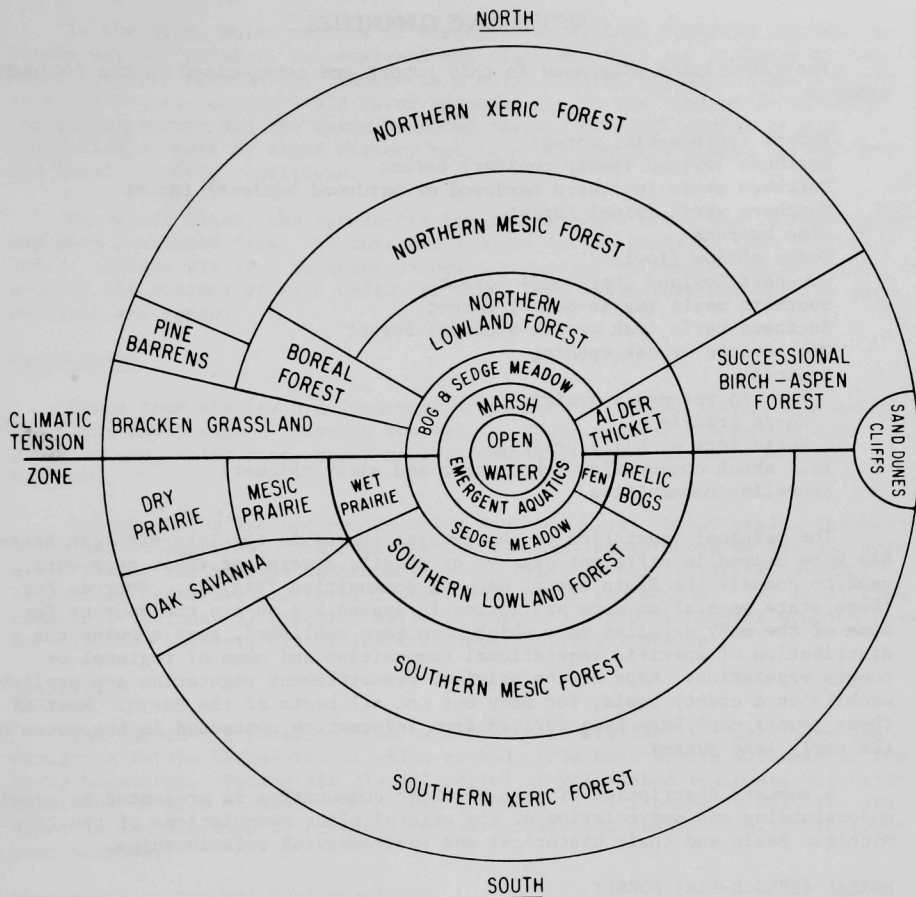
Fig. 3. Schematic Diagram of Moisture and Climatic Relationships of Native Plant Communities of the Lake Michigan Basin. Communities range from wet to dry from the center outward. Similar communities are placed near each other where possible.

NATIVE PLANT COMMUNITIES

The communities discussed in this report are categorized in the following groups:

Boreal (spruce-fir) forest
Northern lowland (swamp conifer) forest
Northern mesic (northern hardwood or hardwood hemlock) forest
Northern xeric (pine) forest
Pine barrens
Sedge meadow (lowland)
Southern lowland (hardwood) forest
Southern mesic (maple-beech) forest
Southern xeric (oak or oak-hickory) forest
Oak savanna or oak opening
Prairie
   Wet and wet-mesic prairie
   Mesic prairie
   Xeric (dry or hill) prairie
Tall shrub communities (shrub-carr and alder thicket)
Shoreline communities

The original vegetation of the several states in the Lake Michigan Basin has been mapped in different degrees of detail; several of these maps were used to compile the Basin map of natural communities (Fig. 2). Sources for these state vegetation maps are listed in Appendix A as are the sources for some of the many detailed maps which have been published, some showing the distribution of specific vegetational communities and some of regional or county vegetation. Maps of the original presettlement vegetation are available, usually on a county basis, for many but not all parts of the Basin. Most of these county maps have been derived from information contained in the notes of the early land survey.

A summary description of each of these communities is presented to provide understanding and appreciation of the natural plant associations of the Lake Michigan Basin and their historical and environmental relationships.

BOREAL (SPRUCE-FIR) FOREST

General Aspect and Structure

Viewed from a distance, the original spruce-fir forest seemed an unbroken dark green sea which, on closer view, appeared as a surface of tightly packed narrow-pointed spires of spruces intermixed with the somewhat broader pyramidal crowns of firs. The occasional clump of yellow birch and maple or white pine indicated some topographic or soil variation, and patches of aspen and white birch indicated disturbance.

Within the forest, the evergreen cover cast a deep and almost unbroken shadow on the ground, save where an occasional tree had succumbed to disease or wind damage. Under the conifer canopy, the understory was scanty or lacking, and the soil was covered with a layer of needle litter and dead branches. Lichens were abundant on the limbs of standing trees and on stumps and logs in openings.

In the cold, moist regions of Wisconsin along Lake Superior, spruce-fir stands may now persist, but eastward and southward they are replaced by northern mesic forest. Presumably, climate is a major controlling factor and a shift to a few degrees colder would favor spruce-fir. At the time of settlement, the boreal forest and the mesic hardwood forest formed a complex mosaic, controlled in part by stand history but to a considerable degree by moisture and local climatic conditions.

On wetter sites, the spruce-fir forest may grade into, and in some cases may have developed from, the northern lowland (swamp conifer) type (Curtis, 1959). Balsam fir is a frequent understory species in several forest types and, in the absence of fire, often replaces less shade-tolerant species such as birch and aspen.

Composition

Seven tree species are important components of boreal forest stands in the Great Lakes region (Maycock and Curtis, 1960). These are balsam fir, white spruce, white pine, sugar maple, trembling aspen, white cedar, and hemlock.

Common shrubs include round-leafed dogwood, hazel, honeysuckle, thimble-berry and blueberries. The common herbs are similar to those of the northern mesic forest and include Canada mayflower, dwarf cornel, bigleafed aster, bluebeads, bedstraw, and several species of ferns and sedges. The total tree component includes 32 species, while 56 shrubs and 240 herbaceous species have been listed; however, only a few are important in all stands.

Floristics

The spruce-fir forest of the Lake States is similar in composition and structure to the boreal forest which extends from Nova Scotia westward to the Rocky Mountains. During the glacial period it was pushed southward but often continued to grow close to the border of the ice. Its presence near the ice front is demonstrated by numerous buried forests and abundant pollen in lower peat samples.

Resistance to Natural Perturbations

Catastrophe is a common event in the boreal forest, and may result from wind, fire, or spruce budworm infestation. Entire stands may be destroyed and rapidly replaced, forming large areas of even-aged forest. Fir and spruce are shallow-rooted, but fir is more susceptible to wind throw and to decay than is spruce. After fire, stands of white birch and trembling aspen often develop to form a brief intermediate stage under which spruce and fir seedlings may develop. Curtis (1959) noted that jack pine and black spruce may also develop following major disturbance.

Both balsam fir and spruce are susceptible to damage and widespread mortality by epidemics of the spruce budworm (*Archips fumiferana*), especially when the stands are extensive. Several heart-rot fungi also hasten the death of fir.

Environmental Relationships

The boreal forest receives plentiful summer rainfall and generally has cool temperatures even in midsummer. Evapotranspiration is low, and the climate generally moist. Very rarely does the surface soil beneath the forest dry out.

Spruce-fir stands are found on a variety of soils ranging from sands to clays. The soils are generally podzolic, acidic (pH 4-6), often poorly drained, and relatively low in nutrients.

Both spruce and fir have relatively low nitrogen and phosphorous requirements and thrive on poor sandy soils. Vegetational debris returned to the soil is deficient in bases, creating an acid mor or raw humus which forms a Podzol profile.

Distribution

Boreal forest was extensive in northern Wisconsin, but within the Basin, it occurred only in a small area on the northern tip of Door County Peninsula. In the Lower Peninsula of Michigan, boreal forest was present at the extreme northern tip west of the Straits of Mackinac. In the Upper Peninsula, larger areas occurred east and west of Manistique in Schoolcraft County and in a band northwestward from Escanaba in Delta County.

NORTHERN LOWLAND (SWAMP CONIFER) FOREST

General Aspect and Structure

Curtis (1959) grouped the northern lowland forest of Wisconsin into wet and wet-mesic segments. These categories apply equally well to Michigan. The wet segment is usually dominated by black spruce or tamarack forest while in the wet-mesic community white cedar and balsam fir are most often dominant with a liberal mixture of such species as black ash, hemlock, yellow birch, and elm.

Tamarack and black spruce accounted for most of the crown cover of the northern wet forests, often growing in dense clumps or presenting a solid canopy, but with the forest interrupted by areas of open shrubby bog.

The conifer (tamarack) swamps in southeastern Wisconsin and in the southern half of Michigan's Lower Peninsula are assumed to be relics from the earlier postglacial period. In these "outliers" of northern lowland forest the bog mat supports many species normally found only in northern bogs as well as many northern mesic-forest species.

The northern wet lowland forest with its clumps of dark-green pyramidal spruce intermixed with groups of the more open and irregularly branched tamarack, set in a matrix of low shrubs, and often with a fringing backdrop of hemlock, white cedar or pine, is universally intriguing and esthetically attractive. The golden fall coloration of the tamarack provides a striking contrast to darker evergreen conifers. Fall color is augmented by patches of birch, aspen and red maple bordering the bogs.

The northern wet-mesic forests include a variety of tree species, with white cedar usually a major component and often with admixtures of balsam fir, hemlock, elm, black ash, red maple, sugar maple, and broad-leafed shrubs. White cedar usually is aggregated into dense clumps with a complete canopy cover and heavy foliage under which light may be reduced to less than 0.1% of full sun. The dense yellow-green cedar foliage gives a distinctive appearance to these swamps, especially when contrasted to the dark conical fir and the low spreading alder. The two other major species of the wet-mesic swamps, balsam fir and black ash, occur in a dispersed pattern. Hemlock and yellow birch are often found growing on low mounds of mineral soil or on fallen logs.

In the north, tamarack swamp forests did not often exceed 60 ft in height, although they grew taller in the southern part of the Basin. The tops of the tamarack and spruce grow at a uniform level, giving an even profile.

Trees in most wet conifer forests grow very slowly and may reach ages of 50 to 100 years while only an inch or two in diameter. In the wet-mesic stands growth is more rapid; on well-drained sites in the absence of competition, the so-called wetland species--cedar, tamarack and black spruce--are capable of rapid growth.

The northern wet forest may remain stable for centuries but may be succeeded by northern wet-mesic or, under some circumstances, by boreal forest. Species composition of the wet-mesic segment is also relatively stable, but over time it may give way to northern mesic forest.

Composition

As noted above, the northern lowland forest may include several inter-related components. The wet segment or tamarack-black spruce swamp is associated chiefly with a sphagnum-leatherleaf understory typical of the open bogs. The woody shrubs may include cranberries, blueberries, bog birch, and mountain holly while the ground vegetation includes Laborador tea, pitcher plant, various sedges, cotton grasses and a number of orchids.

In the wet-mesic forests the white cedar-balsam fir stand may grade into a mixed stand with black ash, yellow birch, hemlock and American elm and may include as smaller trees alder, mountain ash, sugar and red maple. The ground layer is diverse and abundant, including a wide variety of ferns, small shrubs and herbs. White and jack pine may occur in the wet forest, and white pine in wet-mesic stands.

Resistance to Natural Perturbations

On past occasions, large areas of tamarack have been destroyed by insect attacks, chiefly by the larch sawfly (*Pristophora ericksonii*), a defoliater. This insect caused serious damage in Wisconsin tamarack swamps between 1900 and 1910 and again after 1950 (Curtis, 1959).

Wind may be a major cause of disaster in that all of the lowland conifers are shallow-rooted and readily wind-thrown. The dead dry crowns of wind-thrown trees are highly conducive to fire. Only white cedar has adapted to wind damage; it layers readily and develops new upright trunks. Tamarack produces new stems occasionally by root sprouting.

The moist or wet conditions in these lowland forests generally preclude fire as a factor, but during extended periods of drought, fire can move through such stands as it did during the 1930's. The thin bark of tamarack makes the tree susceptible to fire, and entire stands have been killed. Drastic disturbance by wind and fire sometimes resulted in reversion to a treeless sedge-bog. Severe disturbance often slowed successional change and maintained the bog type for centuries.

Black spruce is fire-sensitive but the cones, growing chiefly on the upper terminal branches, are often only scorched and open to release seed. Curtis (1959) suggested that, in a mixed, closed stand of tamarack and black spruce, a series of catastrophic fires could eliminate tamarack and promote spruce.

Black spruce is attacked by the dwarf mistletoe (*Arceuthosium pusillum*), which frequently occurs in great numbers on young spruce twigs, producing bushy witches' brooms and stunted tree growth.

Raising or lowering water levels can also seriously damage lowland conifer stands killing some or all the trees. Damage of this kind often appears after highway construction in many parts of the Basin.

The wet-mesic swamp was the traditional winter habitat to which the white-tailed deer retreated as the snow became deep. In these cedar yards, deer found shelter from the wind and an ample variety of shrubs which, combined with cedar twigs, were a palatable and readily-available food supply. The combination of logging and regrowth supplemented by restricted hunting stimulated an explosion of the deer population in Wisconsin and Michigan. As the winter populations grew, the yards were stripped of all vegetation within reach. Most cedar swamps today show a browse line at four to five feet above the ground. Deer pressure has reduced or eliminated cedar reproduction in many areas and has reduced vegetational complexity and carrying capacity in these swamps.

Environmental Relationships

Northern lowland wet forests grow on organic or peat soils which are highly acid and continuously wet. Soils of wet-mesic forests are less acid, and are relatively drier and better aerated (Curtis, 1959).

Curtis (1959) suggested that condensation may account for the high densities of lichens and mosses on twigs and logs. In areas with scattered trees, clear night temperatures may frequently drop below freezing during the summer. To survive, bog plants must be frost-hardy.

In the wet forests the sphagnum moss forming the ground cover is a good insulator and slows thawing of the bog in the spring. In the northern bogs ice may be present in June. Thus, in early summer the tops of the plants may be subjected to temperatures far higher than those in which the roots are growing. The heaths (bog laurel, leatherleaf, etc.) may flower while the ground remains frozen (Curtis, 1959). In general, bog plants show adaptations for life in a wet habitat which to the plants is physiologically dry.

The lowland conifer community moderates its own microclimate. Winters may be slightly warmer with less temperature fluctuation than on the nearby uplands, while in contrast, the growing season is cooler and shorter.

Distribution

Northern lowland forests were common in the Michigan part of the Basin, scattered and limited in the southern Lower Peninsula, but more frequent in central and northern parts of the Lower Peninsula. Figure 4 illustrates the distribution of bogs in Emmet and Cheboygan counties in Michigan.

Extensive tamarack, spruce, and cedar swamps covered large areas in the eastern Upper Peninsula, east and northeast of Manistique, and west and north of Escanaba in Delta, Menominee, Dickenson and Marquette counties.
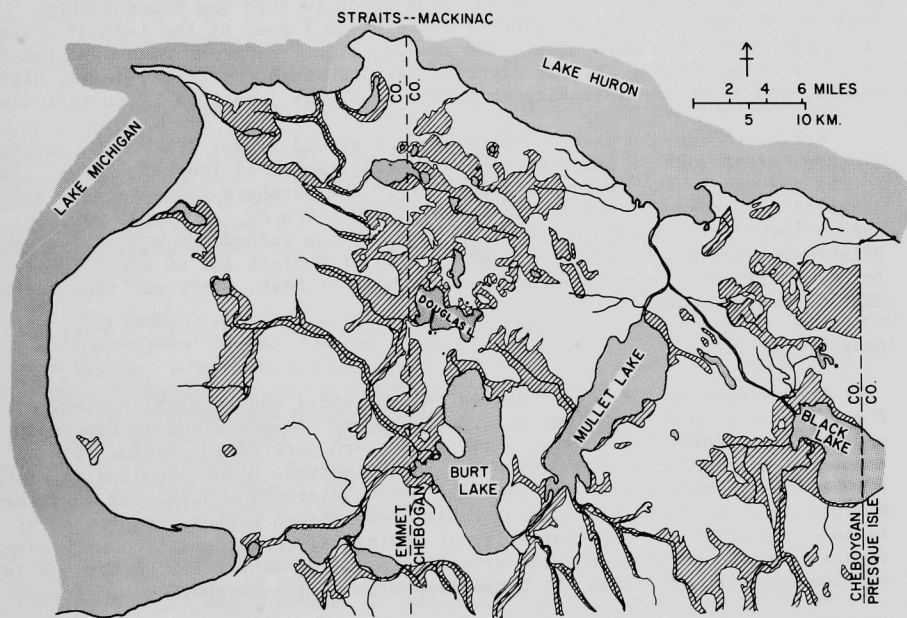
Fig. 4. Bogs in Emmett and Cheboygan Counties, Michigan. Redrawn from Gates (1942). Most of these bogs lie within the Lake Huron Drainage Basin.

In Wisconsin, perhaps 400,000 to 500,000 acres of northern lowland forests occurred in the Lake Michigan Basin on old lake beds and along smaller streams and rivers. Wet and wet-mesic swamp forest was abundant throughout areas of pitted outwash and ground moraine; swamps were perched in depressions of major moraine systems and developed in all the stream valleys from Marinette County

southward. Tamarack bogs were common in southeastern Wisconsin (for example, Cedarburg Bog in Ozaukee County) and some large areas of white cedar and black ash were also present.

Tamarack swamps occurred in the dunes of northwestern Indiana (Pepoon, 1927) and the wetlands of northeastern Indiana (Leesburg Swamp) and were also found in a few limited areas in Lake County, Illinois. These southern outliers of the northern lowland forest represent particular areas of significance in the postglacial history of the Basin.

NORTHERN MESIC (NORTHERN HARDWOOD OR HARDWOOD HEMLOCK) FOREST

General Aspect and Structure

At their prime, the old growth northern hardwood-conifer stands were magnificent forests of large trees. Smaller stems of suppressed maple, hemlock and beech combined with ironwood and blue beech to form the lower canopy. Save for patches of saplings growing in openings formed by the loss of a large tree, the forest was open underneath and the first branches often appeared 60 or 70 ft above ground. Little light filtered through the thick, dense, high canopy, and often the intensity at ground level was less than 1% of full sun.

Spring ephemerals made up the prevalent ground flora; 70% of the species bloomed before June 15 and fewer than 5% after August 15 (Curtis, 1959). Large shrubs and woody vines were not important in the northern mesic forests and occurred either around and in the wetter depressions or, as Canada yew, in dense clumps on favorable slopes. In general, the understory vegetation was relatively sparse and under the dense groves of hemlock and of beech (where found) there was virtually no understory; neither herb, shrub nor tree reproduction was present.

Composition

Composition of the forest varied on both local and regional scales. Beech became less abundant westward in the Upper Peninsula and in Wisconsin and was not present in the stands in the western part of the Basin. Disturbance, particularly ground fire or heavy windthrow often resulted in almost pure stands of yellow birch or hemlock. Major disruption permitted an intermixture of white pine, while more stable areas showed higher proportions of beech or sugar maple. The interplay of biological characteristics with historical events and environmental diversity produced many local variations in species composition within the broad framework of the northern mesic forest.

White pines were often the largest trees in the northern mesic forest, but were rarely found in the sapling layer. The pines stood out over the hardwood crowns and their gnarled tops could be seen for miles. Usually they occurred as single stems or in small groups of large trees, presumably originating in the openings produced by an earlier catastrophe. Yellow birch, hemlock and sugar maple were the characteristic species of the mesic forests of northern Wisconsin and Michigan. Basswood, white ash, and American elm were also present and in Michigan American beech was common. Hemlock, in particular, had a patchy distribution, occurring in dense clumps, often with pine.

Shrubs were not abundant and included Canada yew, elderberry, leatherwood and hazel, while other plants included prostrate, creeping and evergreen vines, i.e., partridgeberry, bunchberry and twinflower. Baneberry, bedstraw, wild licorice, twisted stalk, trillium, several species of club mosses, maidenhair fern, woodfern and other species were common. The saprophytic and parasitic seed plants included Indian pipe, coral root, beech drops and squawroot.

Resistance to Natural Perturbations

The several species of this community respond to natural events in different ways. Openings are often created by windthrow or major "blowdown". These areas may develop into patches of balsam fir, red oak or white pine, particularly if the fallen crowns and litter burn in a lightning-set fire, or if extensive soil mounds are formed by upturned root systems. On the other hand, such wind-caused disturbances, in the absence of fire, frequently increase the dominance of sugar maple. Maple and beech (where beech occurs) reproduction is generally present in abundance. In occupying any opening, the seedlings and sprouts already present have a head start over those seedlings that develop only after disturbance or only on mineral soil.

Windthrow, sometimes augmented by fire, is probably necessary to maintain yellow birch, basswood, American elm, hemlock and white ash in the forest canopy. Basswood usually reproduces by basal sprouting; yellow birch and hemlock reproduce also by seeds germinating and seedlings developing on fallen logs. Fire is not common and occurs only after extensive drought. Thus, opportunities for extensive seedling reproduction of birch, hemlock, pine and basswood are infrequent or rare. Most species are susceptible to windthrow and heart rot.

Young hemlock and yellow birch shoots are very palatable to deer, so that today, where deer populations are high, browsing pressure eliminates effective reproduction. A browsed hemlock seedling rarely develops a new crown; in contrast, browsed sugar maple seedlings resprout vigorously and may persist for many years even with annual browsing. This differential response favors maple and today may serve to hasten the development of pure maple forests. Canada yew is a favorite winter browse plant for deer and this shrub has been almost eliminated from many forests in the Basin. In the presettlement forests, deer populations were limited.

Environmental Relationships

The northern mesic forest is best adapted to cool moist climates and to loamy or clay-loam soils. The ability of sugar maple and other broad-leafed species to obtain nutrients and to develop a rich humus layer permits this community to grow on fine loamy or clayey sands and on rocky areas as well as on deeper rich soils. Clumps of hemlock produce deep layers of acid, needle litter with the resulting strong podzolization of underlying soil.

Distribution

In Wisconsin, the northern mesic forest was the most extensive community; perhaps three to four million acres occurred in the Lake Michigan Basin. At the time of settlement, a narrow band of this forest extended from Milwaukee County northward along Lake Michigan, while large continuous areas were found

from Manitowoc County north into Door County and northwestward throughout much
of the Basin area.

Curtis (1959) noted that sugar maple is abundant throughout the Basin.
In Wisconsin, beech is restricted to the counties along Lake Michigan and
Green Bay, but is more generally distributed within the Michigan part of the
Basin. Hemlock extends westward beyond the Basin as does yellow birch. The
northern mesic forest was absent from Illinois and Indiana but reappeared
midway in Michigan's Lower Peninsula and was extensive in the northern end of
the Lower and in the entire Upper Peninsula.

NORTHERN XERIC (PINE) FOREST

General Aspect and Structure

Much has been written of the vast pineries of Michigan and Wisconsin, and
the prevailing popular picture is one of miles of dense pine forests. Such
forests existed and billions of board feet of lumber were cut and transported
to build Chicago and other cities. However, these forests were far from
uniform.

Pines show rapid height growth and a clear-cut growth form, with a single
dominant central trunk, and relatively limited branching. Such stands often
produced huge yields in both Michigan and Wisconsin [e.g., 100,000 bd ft/acre
(Roth, 1898)]. Jack pine is the least shade-tolerant, red pine intermediate,
and white pine most shade-tolerant. White pine is the largest and longest-
lived tree of the northern stands and, at the turn of the century (1900),
stems of 350 to 400 years old were common.

Pine stands range in character from the dry open forests of jack pine to
the denser, usually more productive red pine stands, to forests of clear-boled
mixtures of red and white, and finally to stands of old-growth white pine,
often with an understory of maple, yellow birch and hemlock.

Most pine stands allow considerable penetration of light. This is
reflected in that (Curtis, 1959) almost 50% of the prevalent forest herbs
bloom between June 15 and August 15, while 40% bloom in spring, and 10% in
autumn.

Composition

Curtis (1959) divided the northern xeric forest into two segments--dry
and dry-mesic forest. In the dry forest, jack pine is more important than red
or white pine, and Hill's oak is a common component. The dry jack pine or
jack pine-red pine segment usually lasts only one generation unless burned and
regenerated. If not disturbed, it may be succeeded by northern dry-mesic
forest. In the dry-mesic forest segment, white pine and red pine form the
overstory, with a lower layer of red maple, paper birch and northern red or
Hill's oak.

Shrubs of the northern xeric forest include American and beaked hazel,
blueberries and occasionally poison ivy. Among the herbs and forbs are wild
strawberry, false barrens strawberry, bracken fern, princess pine, several
asters, cow wheat, dogbane and trailing arbutus, which with many other species
form an open ground cover.

Floristics

In floral affinities, the Lake States pine forests are closest to similar forests of the Appalachian Mountains, although in immediate postglacial time, invasion of the northwestern part of the Lake Michigan Basin may well have been from Minnesota (Wright, 1968).

Resistance to Natural Perturbations

Fire and windthrow are the primary agents of disturbance in a pine forest. Fire was most frequent in the jack pine forests, where needle litter and low branches made the stand highly fire-susceptible. Older red and white pine, if present, often survived fire by virtue of their thick bark and tall, self-pruned trunks. As red maple, birch, oak and other hardwoods enter the stand, fire frequency is reduced and the moisture balance improves. Wind may alter any successional stage in the pine forest, but wind damage was most frequent and produced the most dramatic results in stands of the 100- to 250-year age class. In such stands large numbers of trees were often uprooted.

Drought years often brought crown fires, burning large areas. Such holocausts occurred less often than did ground fires, which kept the forest open by eliminating shrubs and hardwood seedlings. If jack pine was present, a ground fire often provided the heat required to open the cones while it also provided a favorable seedbed.

In the northern parts of the Basin, periods of high humidity may persist for as long as 24 hr. This condition promotes infection by the white pine blister rust fungus, an introduced disease not present in the presettlement forests but now widespread. Aspen was usually present in the pine forest, but is a short-lived tree susceptible to aspen canker and other diseases.

Environmental Relationships

Curtis (1959) noted that, ".... *The light intensity on the forest floor decreases as shade tolerance of the dominant species increases, with maximum light in the jack pine stands and minimum readings in the white pine-hardwood intermediate stands.*" Available light influences the dryness of the forest floor as does the interception of precipitation. Only eight-tenths of the total rainfall reaches the ground beneath the pine canopy and interception of snow is probably even greater. Dry conditions in the pine forests are also related to soil characteristics, i.e., especially the excellent internal drainage and low water storage in the sandy soils.

In the pine stands, accumulation of needles produces an acid mor humus. The coarse sandy soils supporting jack pine were not only drier but were considerably less fertile than were the soils which normally supported red and white pine.

Distribution

Northern xeric forest was found in all sections of Wisconsin north and east of the tension zone, especially on outwash sand plains; in the Basin, this area included Marinette, Florence, Waupaca and Menominee counties. It also developed on sandy terraces and floodplains adjoining lakes and streams

throughout the area. The approximate area of northern dry-mesic forest was 1,930,000 acres in Wisconsin, of which perhaps 40% fell in the Basin.

Pine forests were virtually absent from Illinois and Indiana, although a few pine stands were found on the Indiana dunes.

In southern Michigan, white pine forests occurred only near Lake Michigan, mostly on dune sands or in swamp areas. They became more abundant northward, with almost 200 square miles of white oak-white pine forest on a sandy lake plain in central Allegan County (Kenoyer, 1933). North of Allegan in Ottawa County, pine was found near Lake Michigan, while in Kent County, Livingston (1903) noted areas of oak-pine-sassafras. Farther north, vast areas of central Michigan carried prime stands of white and red pine growing, in various mixtures, with hardwoods. In Montcalm County, white pine was intermixed with beech and hemlock; elsewhere oak appeared.

In the Upper Peninsula, pine stands were abundant on the better-drained and coarser soils from Schoolcraft County westward.

PINE BARRENS

General Aspect and Structure

The pine barrens are savannas, characterized by scattered clumps of jack pine often associated with Hill's or black oak amid large open areas of grasses, sedges, forbs and low shrubs. Typically, a group of young jack pines surround an older, often fire-scarred, tree. These tree groupings are scattered at considerable distances from each other so that the stands were sparse; some averaged only two to eight trees per acre (Brown, 1950). The trees are generally small with an average diameter of about three to four inches and an average height of 15 ft. The scrawny appearance and stunted growth reflect the harsh environment. Sweetfern and blueberry, the most prevalent ground-layer species, usually occur in large colonies adding to the patchwork appearance of the pine barren.

Composition

Although jack pine and Hill's oak were the usual barrens trees, they were often supplemented by red pine, black or bur oak, aspen, and choke- or pin cherry, each in some way adapted to fire. Low shrubs and forbs, usually with extensive underground systems, were prevalent and included blueberry, huckleberry, dogbane, sweetfern, dewberry, wild strawberry, American hazel and spurge. Grasses and composites were common.

Floristics

Jack pine and the associated species of the barrens are of northern origin and presumably reinvaded the Basin from nearby areas south and west of the Wisconsin ice.

Resistance to Natural Perturbations

The pine barrens were the direct result of frequent perturbation by fire, often accentuated by drought, which can be particularly severe on deep sandy

soils. If for some reason fire was absent over a period of years, the stand became denser but remained subject to drastic alteration when fire did come. Intensive fire control, practiced today on the jack pine plains, may, in future years of serious drought, provide the setting for a catastrophic conflagration. A hot fire followed by drought conditions could eliminate the pine. However, jack pine generally bears serotinous cones which open only when subjected to heat and may remain on the tree unopened for many years. Development of cones with fertile seed at an early age and the serotinous nature of these cones are adaptations which contribute to the perpetuation of jack pine. Likewise, the oaks produce basal sprouts and sweetfern and blueberry regenerate from underground stems.

The pine barren community depends upon frequent burning for its continuance; without fire it may be replaced by northern dry or dry-mesic forest communities.

Environmental Relationships

The ability of jack pine to regenerate readily from seed and of oak to sprout after fire, coupled with the low nutrient requirements of these species, were characteristics which aided development of the pine barrens community. Since the dry infertile sand plains were frequently swept by fire, burning litter, herbs and young trees, organic matter rarely accumulated in amounts necessary to increase water-holding capacity to permit invasion of less xeric species.

Distribution

In Wisconsin, the pine barrens once covered approximately 2,300,000 acres, chiefly in central and northwestern Wisconsin, generally north of the transition zone (Curtis, 1959). Perhaps 200,000 acres were found in the Lake Michigan Basin where barrens occurred on the sand plains in central Marinette, eastern Menominee and northeastern Florence counties, with smaller patches elsewhere. No true jack pine barrens were found in Illinois or Indiana, although the Indiana dunes provided somewhat similar sites.

In Lower Michigan, pine barrens were present on the sand plains of western Newaygo, Manistee, Lake and several adjoining counties. However, most of these jack pine areas were more heavily stocked and resembled forest more closely than barrens.

In the Upper Peninsula, pine barrens were found on the sand plains of Schoolcraft and Delta counties east, north, and west of Manistique and again in Dickinson and Menominee counties.

SEDGE (LOWLAND) MEADOW

General Aspect and Structure

A sedge meadow is an open grasslike community growing on wet soils with more than half the cover made up of sedges rather than grasses (Curtis, 1959). The sedge meadow often grades into wetter cattail and reed marshes and, on the drier side, into shrub-carr, alder thicket or lowland forest. A variant, the "tussock meadow" is characterized by a somewhat regular distribution of sedge (*Carex stricta*) clumps (hummocks or tussocks) (Costello, 1936).

In spring the wet soils are slow to warm up, thus excluding all but a few hardy spring flowering species. Few of the non-sedge species (less than 25%) bloom before June 15, while 50% bloom in summer, and 25% in autumn (Curtis, 1959).

The peat in southern sedge meadows often contains tamarack logs or cones, indicating earlier presence of conifer swamp forest. Charcoal fragments are also present, indicating that some stands may have originated after fire, perhaps at the time of prairie expansion (Curtis, 1959).

In Wisconsin, the climatic tension zone divides the sedge meadow type into northern and southern components. The species composition is similar despite the climatic differences. The southern sedge meadow is relatively stable but, unless burned, it is invaded in time by various shrubs forming a shrub-carr. The northern sedge meadows are also fairly stable but are slowly invaded by alder. Fire may set development back to aquatic plants or nettle.

Composition

Southern sedge meadows are composed predominantly of sedges (especially *Carex stricta*) with an intermixture of blue joint grass and many forbs, including bugleweed, asters, swamp milkweed, joe-pye weed, boneset, meadow rue, angelica, and other species (Curtis, 1959).

In the north, sedges are also dominant, but bulrush was abundant and goldenrods and asters were the conspicuous forbs.

Sherff (1912) reported that a sedge meadow community in the Skokie Marsh near Chicago had 113 species, of which 84 were on the list from Wisconsin meadows (Curtis, 1959).

Floristics

Curtis suggested that the northern sedge meadows had floristic ties with the sphagnum bogs, while the southern meadows showed similarities to the wet prairies.

Environmental Relationships

Climates of sedge meadows are characterized by lower temperatures, less evaporation, and shorter growing seasons than for the adjoining upland. Lack of water is rarely limiting, although excess water often creates difficult growing conditions for many plants. The ground is often flooded in the spring or after heavy summer rains.

Sedge meadow soils often are deficient in oxygen and under reducing conditions may produce methane or other "marsh gases" (Curtis, 1959). The soils range from raw sedge peat most common in the north to peats or muck resulting from decomposition of sedge peat in the south. Erosion of the surrounding uplands may add considerable mineral matter. However, boron, copper, manganese and other trace elements are often lacking.

Distribution

Sedge meadows were commonly present in poorly drained sites throughout
the Lake Michigan Basin. The northern meadows usually occurred in narrow
bands along streams or lakes, lying between the emergent aquatic community and
the developing alder thicket. In the southern part of the Basin, sedge meadows
were often extensive and occupied peat-filled depressions which may earlier
have supported lowland forest. The meadows are often associated with prairie
or oak or pine savannas further suggesting the importance of fire in their
development and maintenance.

SOUTHERN LOWLAND (HARDWOOD) FOREST

General Aspect and Structure

From the vantage point of a hill overlooking a river valley or looking
inward from a river flowing through lowland hardwood forest, the stands seemed
as a continuous lush mass of vegetation. Sometimes the forest edge would
appear as a dense growth of shrubby smaller trees and brush, but often the
channels and the abandoned meanders were narrow and the banks were heavily
shaded so that one could look directly into an open forest. The trees were
often very large, with several to many stems and huge, spreading crowns.

The larger size of trees, rather than high densities, produced stands
with high basal area (avg. 98.6 ft^2/acre). Expanded crowns maintained complete
canopy coverage even with low stem density (avg. 85 trees/acre). Curtis
(1959) spoke of a strong resemblance between the canopy base of the southern
lowland forest and the arched and vaulted ceiling of a cathedral.

The lowland forests of river bottoms are often flooded, primarily during
spring. There are few spring blooming species. Since the flood period varies,
the dominant groundlayer may change from year to year. Curtis (1959) noted
that the groundlayer reaches maximum growth in August, and that in different
years, the dominant species might be either woodnettle, jewel weed, or nettle.
In contrast, in more mesic hardwood swamp forests, where flooding rarely lasts
into June, an abundant spring flora may develop.

Composition

The southern lowland forests have a greater variety of trees than any of
the other natural communities of the Basin. Species composition varies.
American elm, silver maple, green ash, cottonwood, swamp white oak, and willow
are the dominant species in the Basin (Stearns, 1965).

Woody and herbaceous vines, including poison ivy, woodbine, wild grape,
dodder, wild cucumber, and half a dozen others are prominent in the lowland
hardwood forests (Curtis, 1959). Woody shrubs are infrequent; of these button
bush, wahoo, and silky dogwood were the most common. Curtis (1959) listed the
nettles, jewel weed, sedges (37 species of *Carex* alone), and several grasses
and various Umbelliferae as common ground species.

Floristics

A large number of trees in the southern lowland forests are of southern origin and entered the Lake Michigan Basin from the Mississippi River drainage basin along the river valleys. These trees include the smooth buckeye, hackberry, river birch, honey locust, and sycamore. For species diversity, the river lowland forests of northern Illinois and Indiana were probably the richest in the Basin.

Ware (1955) noted that hybridization between tree species was common in the bottomland forests. Conspicuous examples in the Basin included the green ash-white ash complex in eastern Wisconsin, the red maple-silver maple hybrid of the Wolf River drainage basin, and the balsam poplar-cottonwood complex near Green Bay. Ware suggested that the vigor and adaptability of the lowland forest trees make them especially useful for urban planting.

Resistance to Natural Perturbations

Most lowland hardwoods reproduce infrequently by seed. Conditions for germination are frequently poor, due to flooding. Successful seedlings may be destroyed by flash floods or by long periods of submergence; thus, stems of younger trees are less frequent than they are on upland sites.

Damage to the base of tree trunks by ice and other flood-carried debris apparently contributes to the abundance of multiple-stemmed trees.

Fire is uncommon in the lowland forests, but all species except willow are moderately or highly resistant to fire. Windthrow, undermining by water, and deposition of silt were common causes of disturbance.

Frequent flooding and the low timber value of lowland hardwood species have saved many of these stands from destruction. Grazing is common and may affect composition by favoring the "weedy" species. Today, tile drainage and grazing may influence both growth and species composition. The wet-mesic stands may also be seriously affected by prolonged flooding.

Environmental Relationships

In Michigan and Indiana, lowland hardwoods are widespread on flat, poorly drained soils. The river forests (commonly called bottomland or floodplain forests) and the lake or swamp border types (called hardwood swamps) are similar in that they have a continuous soil moisture supply well in excess of precipitation. They differ in that the bottomlands receive silt from spring floodwaters while the lake plains do not. Likewise, the bottomlands show the greatest fluctuation in soil water ranging from actual submergence during flood times to almost xeric conditions during midsummer. The constant water supply of the hardwood swamps permits accumulation of considerable soil organic matter.

Distribution

Lowland hardwoods were found in river valleys, old depressions, and lake plains. The original southern wet forest in Wisconsin was limited to valleys along the Fox, Wolf, and Milwaukee rivers. A few stands occurred along the

Sheboygan and Manitowoc rivers. Many extinct glacial lakes and poorly drained areas, especially in Waukesha and Dodge counties, were occupied by hardwood swamps.

In Illinois, stands resembling those of Wisconsin were found only in the north (Telford, 1926), but chiefly south and west of the Lake Michigan Basin.

In lower Michigan, the southern hardwoods were found in the valleys of the Grand and the Kalamazoo rivers. The poorly drained filled or persisting lake beds, especially in Oceana, Midland, Salina and Newaygo, and to a lesser extent in Montcalm, Allegan, Eaton, Kalamazoo and Calhoun counties, were covered by the southern hardwood forests.

SOUTHERN MESIC (MAPLE-BEECH) FOREST

General Aspect and Structure

The maple-beech forest was an important and widespread presettlement vegetation of the Lake Michigan Basin. The interior of the older, well-developed forest resembled a huge green-domed room with subdued light and a sparse understory.

In openings resulting from the death of one or two trees, seedlings of beech and maple developed into a sapling stand which rapidly filled the opening. The lower branches were quickly self-pruned, and in the old stands, branching began 50 or 60 ft above the ground. Stands were not uniform. Smaller maples, beech and species such as ironwood were present in these patches. Where there had been a disturbance more general than the loss of one or two trees, the stand often included less shade-tolerant species, such as black cherry, basswood, elm or red oak; these often developed with the maple and beech to form a high canopy.

In Michigan, as in Wisconsin, the maple-beech forest was distinguished from the northern mesic forest by a general absence of conifers and of yellow birch; these latter species usually occurred in relic northern wetland types to the south of the climatic transition zone. The transition zone, as an area of climatic, vegetational (Curtis, 1959) and edaphic (Veatch, 1932) change, effectively delimits northern from southern mesic forest (Fig. 1).

Ground vegetation was usually sparse, except during the brief spring period. Ephemeral species grew rapidly in the spring, frequently while the snow was still melting. Flowers and leaves often appeared simultaneously. By the time the trees were in full leaf, the ephemeral herbs had died back with little trace of leaves or fruit.

Composition

Although generally similar in composition, the southern mesic forests show geographic variations across the Basin. Beech, an important species in Indiana and Michigan, was and is present in southern Wisconsin only near Lake Michigan. In contrast, basswood, of less importance in Indiana and Michigan, is an important species in southern Wisconsin. Hemlock appears with beech and maple in stands near Lake Michigan. Slippery elm, red oak, and ironwood are common associates in the forest in Wisconsin, while American elm

was more frequent in Michigan and white ash in Indiana. Throughout the region, there is a continuum in species composition with no ready criteria for identifying discrete communities from the tree composition (Curtis and McIntosh, 1951). The ground cover includes a great variety of spring flowering species, most of which reproduce vegetatively as well as by seed. These include blood root, hepatica, wild ginger, trillium, meadow rue, violets, and similar herbs. Shrubs are common and include woodbine, poison ivy, gooseberry, and bittersweet.

Floristics

The maple-beech forests of the Lake Michigan Basin have close similarities to the rich mesic forests of the Appalachians and of the Ozarks. Braun (1950) and others have compared species lists and demonstrated similarities in structure. Composition of these mesic hardwood forests, as Curtis (1959) noted, appear very similar from western New Jersey to Minnesota and southward to the Ozark hills and the southern Appalachians. Species of these forest communities had time to become closely adapted to their position in the deeply shaded forest during the Quaternary period.

Resistance to Natural Perturbations

Wind, fire, drought, ice, and disease were the major factors affecting the southern mesic forest. Ice damage was fairly common, usually resulting in broken limbs and tops which in turn permitted infection by fungi, resulting later in breakage or death. As in the northern mesic forest, major fires were not common and were usually associated with protracted drought or wind damage. However, fires in adjoining prairie or oak forest often penetrated into the maple-beech forest.

The southern mesic forests were susceptible to ground fires during the spring before "greenup", and especially during the autumn after leaf fall. At these times, fire would run through the litter and, if sufficiently hot, could injure or kill many trees, since most species present are relatively thin-barked. Sugar maple is particularly susceptible to fire injury.

Wind was responsible for considerable damage. Trees with large crowns and wide spreading branches are subject to windthrow or, less frequently, to wind breakage. In Indiana, Michigan, and Wisconsin, the southern mesic forest lies in those areas where tornados occur with moderate frequency; such storms may cut a clean swath across the forest.

Catastrophic destruction of the canopy by insects, disease, wind, or lightning permits seedlings of oak, black cherry, and other shade-intolerant species to become established. The degree of success of the intolerant trees and, hence, the degree of species mixture is proportional to the amount of disturbance. Conversely, loss of one or a few trees usually favor the shade-tolerant beech and maple.

Environmental Relationships

The southern mesic forest developed on loamy and silty or clayey soils with high waterholding capacity and moderate to good drainage. Soil conditions often improve under maple-beech cover. Leaves of maple, basswood, and other species contain large amounts of calcium, magnesium, and potassium; these

minerals are leached from the leaves and held in the base exchange fraction of organic and mineral material (Youngberg, 1951). Forest growth often resulted in an increase in nitrogen, phosphorus and potassium in the surface layers. Beech and oak are less effective than maple in this "nutrient-pumping."

The southern mesic forest is adapted to the less extreme climates of south-central Wisconsin and Illinois, and southern lower Michigan. Wind movement and air turbulence under the canopy of a southern mesic forest are reduced to perhaps one-tenth of that in openings outside the forest. Thus, humidity increases (10 to 32% higher) and evaporation drops (to one-tenth to one-third) in relation to conditions in the open. Little light penetrates the canopy, save for occasional sun flecks.

Distribution

Stands of southern mesic forest were extensive in the lower Lake Michigan Basin. In northeastern Indiana, the maple-beech forest occupied extensive acreages of Noble, LaGrange, Elkhart and St. Joseph counties. In southern Michigan, maple-beech forest formed extensive, irregular stands in Van Buren, Ottawa, Oceana, Mason, Kent, Ionia, Eaton, Ingham, and Gratiot counties. In Wisconsin, the largest areas, which totaled over one million acres, were in Milwaukee, Ozaukee, Washington, Sheboygan, Calumet, and southern Outagamie counties. Maple-beech forest in Illinois was limited to small stands in sheltered ravines in Lake and Cook counties.

SOUTHERN XERIC (OAK OR OAK-HICKORY) FOREST

General Aspect and Structure

The southern xeric forests of the Lake Michigan Basin were relatively open stands of oak trees, permitting sufficient light penetration which supported a varied and vigorous ground flora of herbs and shrubs. The oak stands showed diversity dependent upon the nature of the site. Oak forest was found on the drier soils and exposures. In southeastern Wisconsin and Illinois it often graded into either oak savanna or mesic forest. The extensive oak forests of northwestern Indiana and southern Michigan usually contained a considerable intermixture of hickory, cherry, and other species.

Sufficient year-round light on the ground sustained a relatively large number of summer and autumn flowering plants. These herbs were also taller than the groundlayer species of most forests and often showed luxuriant growth.

Abundance of shrubs was a conspicuous feature of the southern xeric forest. Thorny species like blackberry, gooseberry, and prickly ash often made the thick shrub layer difficult to penetrate. Shade-intolerant tree seedlings (including oaks) did not survive where the shrub growth was thick.

Black cherry (*Prunus serotina*) was often present in great numbers in the seedling and sapling classes, and other mesic forest trees occurred especially in moist pockets and locations protected from fire.

Composition

Curtis (1959) divided the Wisconsin southern xeric forests into dry and dry-mesic segments. This division is perhaps less apparent but equally

applicable in Indiana and Michigan. The dry segment in Wisconsin was dominated entirely by oaks and, in the absence of fire, was transient and was quickly replaced by more mesic types. The dry-mesic forest usually included an admixture of hickory, sugar maple, and basswood, and occasional other species such as hackberry and black walnut.

Shrub species include gray dogwood, hazelnut, blackberry, and gooseberries. The ground vegetation includes such legumes as tick trefoil and hog peanut, many lilies, composites, and grasses as well as members of additional families including buttercups, rosaceous plants, primroses, honeysuckle and umbellifers.

Wisconsin and Michigan forests were similar in composition. In north-western Indiana and northern Illinois, many oak stands included a greater intermixture of hickory suggesting a similar dry-mesic character.

Resistance to Natural Perturbations

Along the prairie forest border, fires often prevented development of true oak forests with the result that oaks survived as scattered clumps of trees which were infrequently augmented by sprout or seedling reproduction.

Oak trunks are often damaged by ground fires, but the root crown has great powers of regeneration. A mass of stump sprouts usually appears after fire. Additional fires merely stimulate sprout production, reducing the tree to a bush; thus the name scrub oak is sometimes given Hill's oak (*Quercus ellipsoidalis*) (Curtis, 1959). Black oak responds to fire similarly to Hill's oak. The bark of bur oak is thick and resistant to fire, but when the stem is killed, the stump sprouts vigorously. White oak is intermediate in fire resistance and sprouts less readily. Red oak is more susceptible to fire damage than other species.

Several defoliator insects occasionally cause serious damage to oaks. In Wisconsin, a now widespread fungus disease, oak wilt, was present and locally caused serious destruction. This disease apparently did not reach Indiana or Michigan before European settlement. It has probably been active in both states since about 1930, and is often highly destructive.

In postsettlement time, grazing helped to slow the invasion of maple and other species just as fire did earlier. Soil compaction resulting from grazing is also detrimental to oaks. Long-term grazing in these oak stands may convert them into an oak savanna with bluegrass sod.

Environmental Relationships

Oak forests were generally found on well-drained sites, on coarse sandy or light soils, on ridges and on exposed south- or west-facing slopes. Curtis (1959) pointed out the considerable hybridization existing between species within the black and white oak groups. In the black oak group, Curtis (1959) lists Hill's oak as adapted to the driest and least fertile soils, black oak as occupying intermediate sites, and red oak requiring high moisture and relatively fertile soils.

Among the white oak group, bur oak shows a wide range of adaptation to moisture and nutrient conditions, great resistance to fire, and no tolerance

to shade. White oak is somewhat shade-tolerant and has a broad range of moisture tolerance, but is less fire resistant and has a more restricted tolerance than bur oak. Swamp white oak is not found in the dry or dry-mesic types, but rather in the southern wet forests where in other respects it behaves much like white and bur oak.

In the forest, oak leaves accumulate to form a mulch layer several (two to three) inches thick. Oak leaves are relatively low in nutrients as compared to maple, and decompose more slowly. The duff layer usually shows greater acidity (a result of the tannic acids in oak leaves) in the mesic forest.

The oaks are characteristically slow-growing and long-lived. This is especially true of bur oak, which often survives for three or four hundred years.

Distribution

The most extensive oak forests in Wisconsin were found outside of the Lake Michigan Basin. Smaller patches appeared at the western edge of the maple-beech forest in Dodge and Fond du Lac counties and were associated with oak savanna in parts of Washington, Ozaukee, Milwaukee, Marquette, Green Lake, and Waushara counties. Oak savanna, maintained by fire, was much more common than oak forest in southeastern Wisconsin and northeastern Illinois.

In lower Michigan, oak forests were extensive, occupying much of the southern third of the state and extending northward in Kent, Montcalm, Newaygo, Lake, and Manistee counties.

Oak and oak-hickory were widely distributed in the Indiana portion of the Lake Michigan Basin and occupied well-drained soils. The community covered major portions of the northern tier of counties and was interfringed with maple-beech forest, prairie, lowland forest, and wetlands (Lindsey, 1961).

OAK SAVANNA OR OAK OPENING

General Aspect and Structure

Savanna is best described as grassland dotted with clumps of trees or with extended bands or islands of open forest. Savanna vegetation occurs throughout the world, differing in species but with similar aspects. It represents the interface between forest and grassland and is often maintained by fire, cultural activity, or climatic change. In the southern part of the Lake Michigan Basin, oak-opening or oak savanna occupied extensive areas.

Oak openings or oak savanna have been described as:

> "*thinly timbered country interspersed with forests and prairie*" (Peters, 1970).

> "*The oak openings covered with trees about as far apart as in a common orchard.... The bur oaks have tops somewhat resembling the apple tree in form....*" (Bayley, 1954).

Fennimore Cooper, from his 1848 novel, *The Oak Openings*
(abstracted from descriptions selected by Curtis, 1959),
*"The trees were of very uniform size being little taller
than pear trees, which they resemble a good deal in form;
and having trunks that rarely attain two feet in diameter....
In places they stand with a regularity resembling that of
an orchard; then again, they are more scattered and less
formal, while wide breadths of the land are occasionally
seen in which they stand in copses, with vacant spaces, that
bear no small affinity to artificial lawns...."*

Peters (1970), in examining the oak openings in Kalamazoo County, Michigan,
found that the first settlers chose the edge of the openings near the prairie
or locations within the oak openings. He noted that the settlers believed
that the soil of the openings held up longer under cultivation than did the
prairie soil. Also, clearing was far easier than in the "heavy timber" of
beech and maple found on the heavier soils.

Whitford and Whitford (1956) suggested that because of the trees pro-
viding firewood, building material, and fence posts; the belief of many
settlers (erroneous) that the land without trees was less fertile; and because
much prairie sod was too tough to break easily and too wet to plow, the
settlers chose savanna rather than prairie in Wisconsin and Illinois.

Curtis (1959) noted that, *"Generally speaking, all of the trees in a
particular stand are of the same size and age, although the age may vary from
forty or fifty years to over two hundred years. The trees are open-grown with
large lower branches which frequently sweep close to the ground."*

Tree density varied greatly—from only one or two trees per acre to an
open forest. The line between forest and savanna was set arbitrarily in Wis-
consin studies as a tree canopy coverage of 50% or less for savanna (Curtis,
1959).

Composition

On fertile, loamy, upland sites, oak openings were dominated by bur oak
and mesic prairie species, especially grasses, in the understory. On lowland
sites, swamp oak dominated and wet-mesic prairie species provided the under-
story. Scrub oak barrens, on infertile sands, were dominated by Hill's oak
and had an understory of dry-mesic prairie species. North of the climatic
tension zone, scrub oak barrens gradually gave way to jack pine barrens. Two
hundred thirty-two species are represented in Wisconsin savanna and include 18
trees, 23 shrubs, and 191 herbs. Legumes, grasses and composites were the
most common herbs and forbs.

Floristics

The oak openings may have developed from preexisting forest by selective
action of fires that almost annually swept the prairie and which penetrated
into the adjoining forest. Soon after European settlement, many oak savannas
reverted to oak forest, since "breaking" the prairie halted the spread of
fire. Continuous grazing is responsible for most of those stands that remain
as oak openings today.

Resistance to Natural Perturbations

Bur oak is highly fire-resistant because the cambium is protected by a thick corky bark. Bur oak stumps readily produce sprouts when the top is killed. Larger stems (over 6 in. dbh) of Hill's oak also survive fire and produce abundant sprouts giving rise to oak clumps. Black oak is more susceptible to fire than either bur or white oak. The community is very stable in the presence of fire. Without fire, the oak savanna quickly converts to oak forest (Curtis, 1959).

Environmental Relationships

In southern Michigan, oak openings were found on well-drained sandy soils of outwash or morainic material. They were intermixed with swamps, marsh, and lowland forest, as well as prairie and maple-beech forest. The continued existence of oak savanna in Michigan, as in Wisconsin, Illinois, and Indiana, depended upon periods of drought in spring or autumn when fire could readily sweep through the dry prairie understory killing shrubs, seedlings, and saplings. Some savannas appear naturally stable without fire, e.g., the Fox River Valley sandy sites (Whitford and Whitford, 1971).

Distribution

Oak openings were widespread in southern Wisconsin and southwestern Michigan, and occurred in lesser areas in northern Illinois and Indiana. Curtis estimated that oak openings covered 5,500,000 acres of which perhaps 40% were in the Lake Michigan Basin. Oak barrens also were common on the sand plains of central Wisconsin (upper Fox River Valley in Marquette, Green Lake, and Waushara counties). Oak openings in Racine and Kenosha counties occurred on moraines.

Savannas supporting oaks and hickory, but with a somewhat reduced prairie element, were extensive in southwestern Michigan, particularly in Kalamazoo, Calhoun, Case, and St. Joseph counties. In Illinois, savannas were characterized by a bushy strip on the periphery of the stand, often 15 to 100 ft wide, comprised of hazelnut and dogwood, among other species. Indiana oak openings were frequently adjacent to or in upland dry prairie (Petty and Jackson, 1966).

PRAIRIE

Prairie areas of the Lake Michigan Drainage Basin are shown in Figure 5 and described in the following discussion.

WET AND WET-MESIC PRAIRIE

General Aspect and Structure

The lowland (wet and wet-mesic) prairie appears as an open meadow of grasses, sedges, and forbs found in swales and low flat terrain. Most species are aggregated in clumps or colonies. Curtis (1959) suggested that differences in moisture supply caused by slight differences in local elevation are responsible for clumping of wet prairie species. As in the mesic prairie, these aggregates are most conspicuous when different species are in bloom. In the wet prairie, one-third of the species bloom in spring, slightly less than one-half during the summer, and one-fourth in autumn.

38
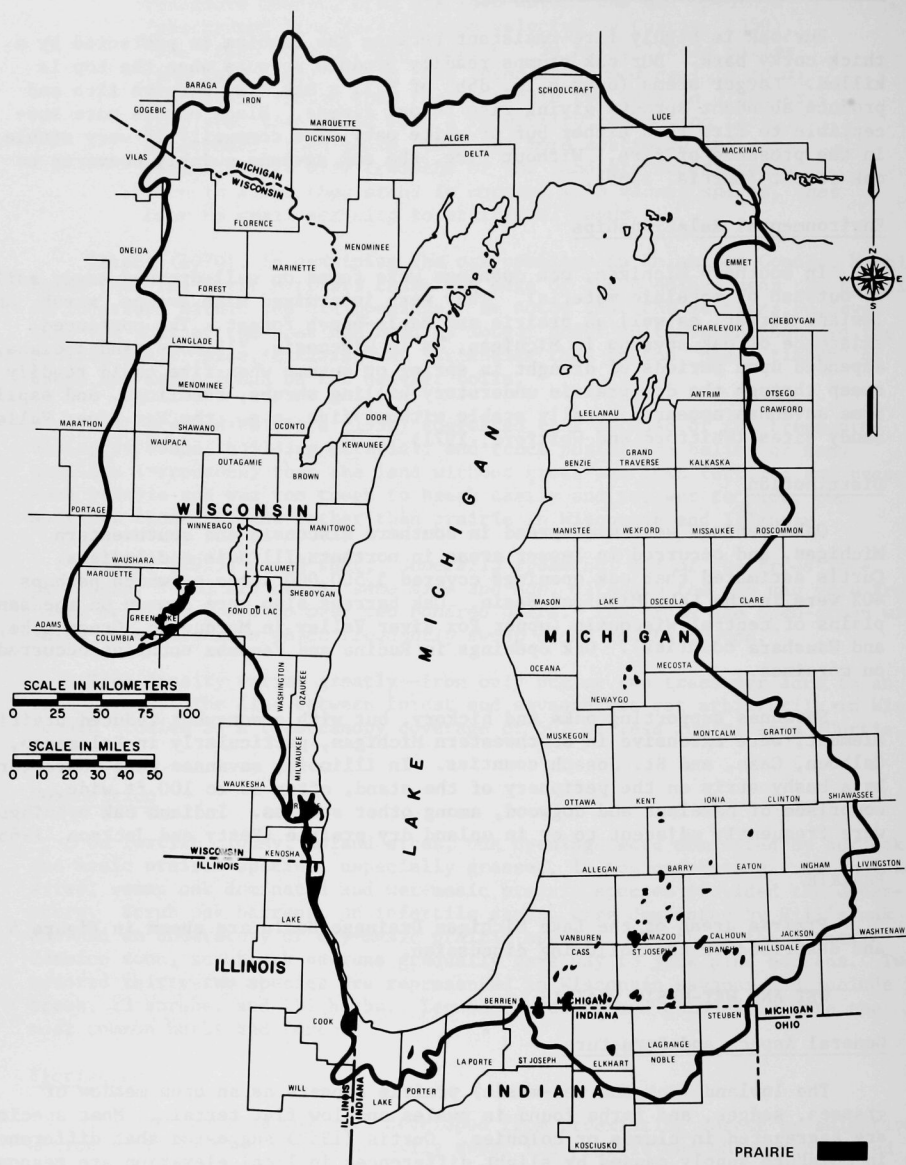
Fig. 5. Prairie in the Lake Michigan Drainage Basin. Compiled from Veatch (1928), Lindsey (1961), Anderson (1970) and Martin (1932).

The wet prairie community includes many species also found in sedge meadow, with the distinction that sedge meadows are dominated by sedges and the wet prairies by grasses. Early accounts by travelers and land surveyors did not distinguish between wet prairie and sedge meadow. The wet prairie is also closely related to the fen, an unusual wet grassland characterized primarily by having a flowing source of water.

The wet-mesic prairie is similar to wet prairie in appearance and is related in species to the mesic prairie. In contrast to wet prairie, many plants of the wet-mesic segment are also found in southern mesic forests and occasionally in southern dry forests. Wet and wet-mesic prairie developed in those sites with tight subsoil and poor aeration which were flooded in the spring, but where, in the late summer, soil moisture fell below the wilting point.

Composition

In the lowland prairie, 51 plant families are represented in both wet and wet-mesic segments; one-half of all wet-mesic species are in five families, and in six in the wet phase. Slough grass is often the major dominant, and bluejoint grass is common. In the Compositae, goldenrods are prominent, as is New England aster, tall sunflower, and compass plant. Prairie dock is abundant. Mountain mint is characteristic of the wet prairie, where fewer legumes are present. The wet-mesic segment may include such species as wild onion, geranium, Jacobs ladder and wild grape.

Floristics

Curtis (1959) noted differences in the floristic affinities of wet and mesic prairies: *"The large Alleghenian meadow element in the wet prairies indicates that this community migrated into Wisconsin* [the Lake Michigan Basin] *from the southeast along with the hardwood forest of similar relationships."* Plants of the wet prairie range toward the southeastern United States. The wet prairies of Illinois, Indiana, and Michigan are very similar. Wet prairie was not common in Michigan, and Brewer (1965) postulated that some Michigan wet prairies may have developed from sedge marshes.

Resistance to Natural Perturbations

The wet prairie was subjected to a regular fluctuation between a wet spring period and a late summer or autumn drought period, often amply dry to carry a hot fire through the dry grasses and forbs. The prairie species were well adapted to this yearly alternation. Neither trees nor sedges could readily invade until man changed the drainage patterns. Major climatic shifts could permit change toward sedge meadow (wetter) or wet-mesic forest (drier).

Environmental Relationships

Lowland (wet and wet-mesic) prairies often developed in the beds of extinct glacial lakes, which accumulated cold air draining down from the uplands on still nights. Growth of the wet prairie plants is lush and rapid, reflecting the hot, sultry conditions that resemble the tropics. The cold air drainage responsible for the summer night fogs also causes late spring and early autumn frosts. Wet-mesic segments were usually located on lowlands subject to flooding after heavy rains or by stream overflow (Curtis, 1959).

In the wet prairies, small differences (a few inches to a foot) in the relief of the underlying soil result in patches better aerated than others. Curtis (1959) stated that differing species responses to aeration produce a mosaic of different species combinations. Brewer (1965) also noted aggregation of species but did not suggest any topographic relationships.

Lowland prairie soils are rich in organic matter and nutrients. The top layers are often similar to peat with much partially decomposed fibrous organic matter. These soils have a high water-holding capacity and low bulk density. A gley layer, indicating poor drainage, is usually present within 30 inches of the surface (Whitford, 1958).

Distribution

Much of the original area of wet-mesic prairie and wet prairie in Wisconsin grew in the poorly drained clayey ground moraine and the low swales along Lake Michigan in Racine and Kenosha counties. It was also found in the Fox River lowlands and near Fond du Lac.

Illinois wet prairies were essentially continuous with and closely resembled those along Lake Michigan in Wisconsin and Indiana. The number of semiaquatic species listed from some Illinois wet prairies led Curtis (1959) to suspect that wet prairies described by Gleason (1901) and others may instead have been sedge meadow.

The wet prairies of northwestern Indiana closely resembled those of Wisconsin and were found in the interdunal swales across northern Lake County and to the south in the Kankakee River basin.

Michigan's wet prairies were limited to a few areas in the southwestern part of the Lower Peninsula. Again, they are similar to wet prairie in Wisconsin and show close resemblance to sedge meadow.

MESIC PRAIRIE

General Aspect and Structure

The mesic prairies were the most luxuriant and productive of the midwestern grasslands. From the air, they appeared as a thick carpet bending easily in the wind. From the ground, they formed a dense jungle of grasses and large, tough forbs.

Many prairie species are grouped into clumps and less well-defined clones, a distribution related to dependence on rhizomes for vegetative reproduction. The grasses of the mesic prairies are well supplied with moisture, grow more vigorously, and reach much greater total heights than the dry or wet prairies (Curtis, 1955). Associated with them are many nitrogen-fixing legumes and several conspicuous composites. The dense grass and forb canopy may average 0.5 to 0.6 m tall in August and reduce light at the soil surface to perhaps 30 footcandles (Curtis, 1959). In September and early October, culms of big bluestem reach an average height of 1.8 m and in favorable years they, along with taller forbs such as compass plant and sunflowers, may reach 2.5 to 3.0 m.

One of the striking features of the prairie flora is the sequence of changing color and aspect as different species come into bloom week by week. From early May, when plants with flowers average under 0.2 m tall, to late August, when compass plants bloom at 2 m or more, height increases. Later in the season height declines to the midheight goldenrods and asters, and the gentians, under 0.5 m, bloom after the first frost (Butler, 1954). Perhaps 50% of the mesic prairie species bloom in summer, over 25% bloom in autumn, and the remainder bloom in the spring. Many prairies exhibit visual dominance of the colorful blooming forbs rather than the grasses. The complexity and diversity of the prairie flora is indicated when remnant prairies of less than 0.5 acre are sampled; 50-75 native species can be listed. A similar area of original prairie probably contained 80-100 different native species.

Composition

The mesic prairie was usually dominated by composites, grasses and legumes, listed in that order, as to number of species. These three families commonly included about 50% of the total species of the prairie and 50 to 75% of the total plant biomass. Curtis and Greene (1949) listed 237 species in 52 families from 65 Wisconsin prairies. From 27 prairie remnants in two counties of southeastern Wisconsin, Whitford (1958) listed 173 species in 45 families.

The common mesic prairie grasses include the major dominant, big bluestem, with little bluestem, Indian grass, prairie switch grass, needle grass, and Leiberg's panic grass. Prominent composites include yellow coneflower, stiff prairie goldenrod, smooth aster, heath aster, common sunflower, blazing star, and compass plant.

Wild rose, wild pea, tick trefoil, wild indigo, wild strawberry, downy phlox, and several other flowering plants were common and characteristic in the patchy, clonal mosaic of the mesic prairie.

Resistance to Natural Perturbations

The prairie was highly resistant to the recurring drought cycles, to the frequent grass fires, and to the selective and migratory grazing of native animals. Today, the moist climate of the midwest has increased the sensitivity of the prairie to disturbance and made it more dependent upon fire to prevent tree and shrub incursion. In recent presettlement time, fire, set by Indians or by lightning, maintained the savanna-prairie border between grassland and forest.

Environmental Relationships

Prairies grow naturally where evaporation during the growing season exceeds available rainfall. Soils and topography appear to be of lesser importance, save near the prairie border. Fire favors grass and represses trees and shrubs at the border of prairie and forest.

Four strongly clumped species, two sunflowers (*Helianthus laetiflorus*, *H. occidentalis*), bedstraw (*Galium boreale*), and finger coreopsis (*Coreopsis palmata*) are known or presumed to produce allelopathic exudates which reduce or eliminate invasion of their colonies by other species. In the case of sunflower, the exudate is autotoxic and suppresses growth in the sunflower

clones (Curtis and Cottam, 1950). Many other mesic prairie species grow in open colonies.

On level or undulating land, the mesic grassland was supported by outwash, glacial till, or residual loessial deposits. The development and fertility of prairie soils reached its peak in the mesic prairie. The deep black topsoil layer was rich in nutrients, neutral to slightly acid, and contained as much as 200 to 300 tons of organic matter per acre. Former prairie areas can be recognized readily by these soil characteristics. Calcium content exceeds that of most forest soils but is lower than in the dry prairie (Curtis, 1959). Conversely, the phosphorus levels are much lower than adjoining forest soils (Whitford, 1958).

Distribution

Mesic prairie and associated oak savanna were important communities in southeastern Wisconsin, northern Illinois, and northern Indiana. The mesic prairies in Wisconsin included 100,000 to 200,000 acres within the Lake Michigan Basin, chiefly in Kenosha, Racine, Fond du Lac and Green Lake counties. Additional areas of mesic prairie with oak openings covered southwestern Milwaukee, Winnebago, and Dodge counties with remnants in the north near Green Bay.

Mesic prairie was common in northeastern Illinois adjacent to the oak-hickory forest. Considerable mesic prairie was found in Indiana, but its exact extent in the Lake Michigan Basin is difficult to determine. At the southern end of the lake, also, some mesic prairie was present. Patches of mesic prairie vegetation occurred in St. Joseph, Elkhart, and La Grange counties.

In Michigan, small patches of mesic prairie were found in St. Joseph, Branch, Calhoun, and Kalamazoo counties (Scharrer, 1971).

XERIC (DRY OR HILL) PRAIRIE

General Aspect and Structure

The term prairie brings to mind broad open plains covered by grasses and populated by prairie dogs, bison, and Indians. Actually, prairies were complex communities with a great variety of plants and animals. In the xeric prairies, the grasses, big and little bluestem, were usually the dominant species, but their growth on dry sites was not luxuriant.

Most species were clumped and gave the prairie a patchwork appearance. Aggregates of any one species were separated by similar aggregates of other species. The grasses filled the gaps and formed a matrix for the clumps. When sunflowers, compass plant and other forbs were in flower, the clumping was very evident.

Prairie in flower is a dramatic sight. In the dry prairie, perhaps one-third of the herbs and forbs flower in spring. Almost half the species, largely legumes and composites, bloom during the summer. Bloom in autumn is likewise striking as the colored network of asters, goldenrods, and gentians appears above the grasses. The dry prairie was commonly found on well-drained sands or on west-facing slopes which warmed and dried early in the spring.

Composition

A relatively few species were abundant; most others were infrequent. Grasses, legumes and composites were the dominant families and, with the addition of the milkweed and the rose families, included over half the species. In addition to big and little bluestem, side-oats grama was a leading grass species. In the dry prairie, little bluestem usually replaced big bluestem as the major grass species, often with needle grass present. Lead-plant, bush clover, azure aster, coneflower, spurge, goldenrod, gayflower, sunflower and prairie clover were frequent. Butterfly weed and Pasque flower were other characteristic species.

Floristics

Species of the dry and dry-mesic prairie are those common in dry grassland westward into the Kansas and Nebraska plains. Dry prairies may have persisted in the driftless area of southwestern Wisconsin throughout the Pleistocene glaciation and invaded eastward when conditions became favorable.

Resistance to Natural Perturbations

The dry grassland was stable and was invaded only slowly by southern dry (oak) forest even when fire was absent. It was influenced chiefly by long-term climatic changes. Minor and local disturbances resulted from concentrations of bison. With the passage of an occasional fire the dry-mesic prairies were also stable, however, without burning, the oak forest invaded these prairies readily.

Environmental Relationships

Xeric prairies occurred on a variety of landscapes, from flat sand plains to very steep slopes. Today, remnants persist on the southwest slopes of steep hillsides where the soil is very thin. These hillsides were most often on limestone or limestone gravels. On slopes, the thin soil limited the water and nutrients for the xeric prairie species. The lower soil water storage capacity, the high insolation, especially on southwest slopes, and the greater wind movement severely restricted plant development. In the Lake Michigan Basin, most dry prairie was found on sands and belongs in the dry-mesic segment. Soil profiles were poorly developed; often the entire soil depth was a uniformly black mixture of organic matter and mineral soil. In limey soils, chert or iron concretions accumulate near the surface. Cool night temperatures provided some moisture through condensation.

Distribution

At the time of settlement, there was little dry prairie in the Lake Michigan Basin. In Wisconsin, a few small dry prairies may have occurred on steep gravel slopes in the Kettle Moraine and on the sand plains and dolomite ridges of the upper Fox River Valley. In northeastern Illinois and northern Indiana, dry prairie was found on the stabilized dunes and the rough end moraines. An intermixture of dry and mesic prairie occurred northeastward through Indiana from southern Lake County into central Porter, northcentral La Porte, and northeastern St. Joseph counties. perhaps extending into Berrien and Cass counties in Michigan. There was also an area of dry prairie in

north central Kosciusko County, Indiana (Lindsey, 1966). Thompson (1972) noted small remnants of dry prairie in Newaygo County, Michigan. In an earlier report, Veatch (1928) mapped the dry prairies of Michigan, including the Big Prairie of Newaygo County, which grew on sandy soil, but he probably also included those better classed as mesic prairie (Curtis, 1959).

TALL SHRUB (SHRUB-CARR AND ALDER THICKET) COMMUNITIES

General Aspect and Structure

Tall shrub communities are found in most wetland areas throughout the Lake Michigan Basin. They are perhaps more common today than at the time of settlement. North of the climatic tension zone these communities are most often dominated by tag alder while in the southern part of the Basin the shrub-carr, largely of willow and red osier dogwood, predominates.

Alder thicket and shrub-carr are similar in exterior appearance and interior structure; the thick shrub growth produces a dense canopy one to four meters above the ground, but stems are irregularly distributed leaving gaps in which the ground surface supports a vigorous growth of sedges, grasses, ferns, low shrubs and herbs. An occasional clump of white cedar or scattered stems of green or black ash or red maple may stand out above the canopy. The uneven distribution of shrub growth and the clumped plants result from variations in reproductive mechanisms, microtopography, soil moisture and disturbance.

In the alder thicket the canopy is usually heavy and, inside the stand, the ground cover is relatively low. However, travel through the thicket is impeded by many living and dead alder stems of finger to wrist thickness. In contrast to the alder thicket, the shrub-carr canopy is less heavy and more irregular, permitting development of numerous herbaceous and woody vines and abundant sedge clumps.

In the shrub-carr, White (1965) described three strata analogous to a deciduous forest; willow and dogwood form the rather open canopy, tall herbs, sedges and grasses form the intermediate or sapling layer (one shrub rarely grows beneath another in a shrub-carr), and smaller plants such as bed straw form the ground layer.

Shrub-carr is an intermediate stage in succession from wet prairie, open fen or sedge meadow to southern lowland forest or conifer swamp. Shrub-carr often occurs only as a narrow band or zone up to 20 or 30 m wide lying between forest and marsh. White (1965) suggested that a particular shrub-carr may be named according to its origin, e.g., prairie-carr or sedge meadow-carr, while the undisturbed lake or stream edge shrub zone may be designated as true shrub-carr.

A large shrub-carr may have a minimum lifespan of 50 years. This period is characterized by slow elimination of sedge meadow species and gradual invasion of forest understory. The shrub-carr is moderately stable when undisturbed and may revert to sedge meadow or fen when burned.

The alder thickets appear to fall in two groups: those that form a narrow band along streams and lake shores and those that are either transitional between northern sedge meadow and lowland forest or that originate after

destruction of the bog forest and serve as a successional stage toward white cedar, conifer swamp or wetland hardwood (black ash-red maple) stands.

Composition

Tag alder is the dominant species in alder thickets. Occasional willow and red osier dogwood are present, especially along the edges of the community. Meadow sweet and current are common low shrubs. Among the herbs, bedstraw, joe pye weed, asters, golden rod and marsh fern are frequent accompanied by a variety of grasses and sedges.

Most woody and herbaceous species of shrub-carrs are common to communities in Wisconsin, Indiana (Youse, 1901) and Michigan (Transeau, 1905; Gates, 1942; Cain and Slater, 1948; White, 1965). The major shrub species may include red osier dogwood, pussy willow, several species of willow, bog birch and meadow-sweet. A sedge (*Carex stricta*) is the most frequent herb. Other common herbaceous species include blue joint grass, jewel weed, marsh fern, swamp golden rod, aster, and bugle weed (Curtis, 1959). In southeastern Wisconsin, White (1965) recorded 192 plant species of which 38 were shrubs. Poison sumac is noteworthy in many stands.

Resistance to Natural Perturbations

Persistance of the shrub-carr community results from the tolerance of shrub species to poorly aerated soil, cool growing temperatures and occasional summer frosts (White, 1965). Trees cannot invade readily under these conditions and the shrub canopy controls development in the understory. Production of vigorous sprouts is an additional competitive advantage especially in response to fire or grazing. Severe grazing creates relatively open stands while mowing and light to medium burning at frequent intervals results in dense sprout stands. Severe fires have resulted in nearly pure stands of nettle or trembling aspen (White, 1965). Occasional burning favors the shrubs which resprout more readily than the lowland forest trees.

Much shrub-carr has been eliminated from lake shores by cottage development and by artificial increases in water levels. Willows are susceptible to the borer beetle (*Cryptorhynchus lapathi*) which weakens and topples stems; however, vigorous resprouting of the willow usually follows (White, 1965).

Alder thickets likewise tolerate considerable disturbance. Alder resprouts vigorously after brush cutting or after light fire. While white cedar and red maple are heavily browsed by deer, alder is not consumed. Without serious disturbance and with freedom from heavy deer pressure, white cedar, black ash, red maple and other trees may invade in openings and gradually overtop the alder. Changes in water level, especially protracted flooding, will effectively eliminate alder thickets.

Environmental Relationships

Both tall shrub communities develop on organic soils in low areas with high water tables and subject to occasional flooding. Summer frosts often occur as a result of cool air drainage into the lower ground combined with poor heat storage in the peat soils. These communities are rarely subjected to water stress.

The soils under shrub-carr are most often peats or mucks developed under either sedge meadow or lowland conifer forest. Alder thickets are more often found on neutral (pH 7.0-7.7), rather than acid, muck soils having some free oxygen and apparently some groundwater movement. These soils may be shallow over till or they may lie over older peat (Curtis, 1959). The soils show a reduced gley layer. Presumably, tag alder (by hosting root nodule bacteria) contributes considerable fixed nitrogen to other species in the community. The moist rich ground layer is prime habitat for ruffed grouse broods dependent upon insects in their early development.

Distribution

Shrub-carr communities occur south of the climatic tension zone; north of the tension zone wet-ground tall shrub communities are typically alder thickets. The majority of modern shrub-carrs in southeastern Wisconsin developed on sedge meadows, which were once mowed by settlers, but are now abandoned. Shrub-carrs (or shrub-fens) in Michigan and Indiana occur in similar habitats.

Alder thickets are found bordering streams and lakes and wetlands wherever present throughout the northern part of the Basin. Large areas of alder thicket grow on organic soils from which the conifer swamp community was removed by logging or fire.

SHORELINE COMMUNITIES

General Aspect and Structure

The vegetation of the Lake Michigan shoreline varies with the extent and type of beach, with the backbeach vegetation, and with the depth of the offshore water. Shallow offshore waters, especially when protected in bays, on windward shores, or in river mouths, often supported wet marsh communities of emergent aquatic plants (Gates, 1912; Sherff, 1913; Waterman, 1917). Sometimes the marsh was flanked by a sandy ridge supporting typical sand beach plants; elsewhere it graded into sedge meadow or lowland forest. In northern areas the transition from wet marsh terminated in sedge meadow with a vigorous sphagnum moss mat.

Along much of the Lake Michigan shoreline, the bottom gradient is relatively steep and the shoreline is exposed to frequent and severe wave action. There beach vegetation developed without a wet-marsh component.

Beach may be divided into lower, middle and upper segments (Cowles, 1899). Lower beach is the zone that lies between water level and the line reached by waves of common summer storms; it lacks permanent vegetation. The middle beach is out of reach of ordinary storm waves and its landward boundary is often formed by dunes; it is sparsely vegetated. Upper beach is the area above normal wave action, often including old beaches from high lake periods; 30 to 40% of the upper beach is vegetated (Cowles, 1899). Landward, the upper beach is bounded by other terrestrial communities (prairie, forest, cultivated land, cities, etc.); it is often separated from these land uses by a clay or till bluff or rock outcrop.

A slight ridge may form a beach pool near the water on the lower beach. These beach pools, especially when associated with streams or runoff water,

provide excellent habitat for algae and for fast-growing shore plants. Algae may also grow on the wet sand of the lower beach and are often abundant on rocks and logs submerged in the lake.

The middle beach is usually sparsely vegetated; it is extremely dry in summer and subject to very high daytime and low nighttime surface temperatures. Plants of the middle beach are usually annuals which germinate rapidly and extend their roots into the moist subsurface sand. Aerial parts grow low to the ground, are often bushy with narrow leaves, and are frequently succulent. Driftwood and other beach debris stabilize areas where plants can germinate and survive to form the focus for small clumps.

The upper beach, farthest from the water, is more stable, has readily available water, and is least affected by wind and waves. Vegetation is often sparse due in part to the low nutrient content of the beach sand. If dunes form, they are found on the upper beach (see section on dune vegetation and succession) and the vegetation changes from grasses, forbs and low woody plants, such as willows and juniper, into the forest stands found on old stabilized dunes. A loose matt of low shrubby evergreen vegetation is the most conspicuous feature of the upper beach, although many grasses, sedges and other flowering plants are present and form a diverse flora.

Composition and Floristics

Plants of the middle beach may include cocklebur, sea rocket and sand bur. Seaside spurge often grows in depressions or pebbly areas. Arrowgrass and sedges are found in the pools.

Many plants are found on the upper beach, including beach grass, sand reed, beach pea, beach cinquefoil and wormwood. Woody plants include bearberry and spreading juniper, while false heather and sand cherry are frequently present. Some species are restricted to the shores of the Great Lakes. Among these endemics, Guire and Voss (1963) listed Pitcher's thistle, found on all shores, dwarf lake iris growing in the north, especially at the tip of Door County, and Houghton's goldenrod which has been reported only on the northeastern shore, especially near Mackinac.

The marshes in the shallow coastal waters included cattail, rushes, bur reeds, sedges, arrowhead, wild iris and other emergent aquatics, while the protected pools had a good assortment of pond weeds, myriophyllum, algae, water lilies and duckweeds. These marshes have been described by several authors, including Gates (1912) and Waterman (1917), and were noted in historical descriptions of Milwaukee, Chicago and Green Bay.

Resistance to Natural Perturbation

When the Lake Michigan level remains stable the marsh communities prosper wherever water depth is suitable and where bars or points protect them from wave action. When water is low the emergent species may be replaced by sedges and grasses or shrubs (often willow or alder), and by wetland forbs. When water levels are high the wet marshes are often almost completely destroyed by submergence and increased wave action.

Waves and shifting sand keep the lower beach free of vegetation. Winter storms usually remove from the middle beach any perennials that may become established. The upper beach is less subject to wind and out of reach of the waves. The matts of low growing vegetation help to stabilize the sand and permit further development of a vegetative cover. A break in the plant cover on a dune may permit the wind to create a "blowout" which again exposes the bare sand surface and permits the dune to shift position.

Of the shoreline vegetation communities, those in protected ponds behind sandspits and those on the stabilized dunes of the upper beach are the most stable.

Environmental Relationships

Shoreline vegetation exists in a rigorous environment, hot and dry or wet and cold and subject to wave and ice action. Surface temperatures may reach 60°C during the day (Gates, 1912) and the surface is subjected to strong drying winds. However, the sand below the surface is usually moist or wet and once plants become established, they usually survive at least until the next severe storm.

Sand and gravel are the major constituents of Lake Michigan beach soil. Plants on these sandy soils are constantly supplied by water by the porosity of the sand and nearness to the lake water table. Sandy soils are deficient in nutrients and organic matter; soluble material is leached out by rain or waves. Solar radiation and wind affect most of the beach unhindered, especially near the water's edge, thereby increasing water loss from the few plants that are present. The anatomy of some beach plants is modified to reduce water loss; others are succulent and retain water. Some beach species survive without modification because of the abundance of water near the surface. Their roots grow in a hydric environment while the tops live in a xeric one. The xeric beach is a microclimatic phenomena; the lake modifies the macroclimate of the adjoining land throughout the year.

VEGETATIONAL CONTINUUM

Plant communities are complex mixtures, each including a vast array of green and non-green plants of several life forms. The forest may include trees, shrubs and herbs, while the grassland will have tall forbs, grasses and low herbs. Each community has a complement of fungi and bacteria, as well as its characteristic mammals, birds and invertebrate animals. Over time communities have evolved into functioning systems adapted to a particular set of soil and climatic conditions and often, also, to natural disturbances such as spring flooding or occasional ground fire. No community can adapt completely to the catastrophic effects produced by events such as protracted flooding, forest fires following extended drought, etc. Following the catastrophic events development of new communities usually begin with pioneer species and gradually change to the community capable of sustained growth under the prevailing soil and climatic conditions.

The initial community to develop, whether following catastrophe or exposure of new ground, will be composed only of those species for which propagules are available and those which can become established on the site at the time.

Propagules arriving later will meet different conditions whether or not they are forced to compete for space, water and light with plants already present. Some species are highly successful in such competition, others are not; for example, sugar maple seedlings develop rapidly in leaf litter where yellow birch will not germinate.

As noted earlier, we chose to describe natural communities as separate and recognizable entities composed of specific combinations of species growing in definable sites. Such an approach is essential to discuss relationships and portray differences. However, in nature it is often not possible to categorize a particular community within the general framework. One finds intergrading communities forming a series between one category and the next. These intermediates result from chances in establishment, site characteristics, weather and history. For example, intermediates between northern wet-mesic and northern mesic forest are frequent as are intermediates between sedge meadow and southern lowland forests. Likewise, the same species occur in different proportions in a variety of communities. For example, basswood is found in the northern mesic forest as well as in the southern wet-mesic, mesic and dry-mesic communities. Species of herbs, shrubs and fungi likewise appear in different plant communities in varying proportions.

The continuum concept of vegetational communities was proposed based on an understanding of the individualistic origin of plant communities and the evidence obtained from field samples of a large number of plant communities throughout Wisconsin (Curtis and McIntosh, 1951). Natural communities are considered to form a continuum in composition with each individual community-- a result of a specific set of conditions. The concept of a continuum is not unique to vegetation but has also been applied to soils; a soil catena represents a continuum of soil types (Bushnell, 1942).

Species composition appears to be the most usable criterion by which to place a community on the continuum. The species present have indeed been selected in part by interactions within the community and in part by relationship to various environmental factors. To use species composition as a criterion, an index was developed to combine several measures of species value; this was designated the "importance value."

Thus the development of each community is an individual process, and as might be expected, the species composition may differ considerably even on similar sites. An aspen-birch forest developing after a major fire might be largely aspen with a few birch, or be predominantly birch, and might or might not include such other species as pin or choke cherry, depending upon the time of the fire, available seed, weather conditions, nature of the soil surface and the intensity of the fire. Similarly, a wet prairie, developing in a swale behind a dune ridge, would be composed of the species available to become established and occupy the area. The individualistic nature of plant communities was proposed by Gleason (1926) and is basic to the concept of the vegetational continuum (Curtis, 1959).

Each species is different from others in its adaptation to such environmental parameters as soil moisture, light quality and quantity, heat and cold and in its individual growth patterns. These individual differences condition the success of the species in the community. Gradual changes in the environment, which occur as the community develops, may alter species responses. Thus each

community is essentially unique. However, out of a great many species, there is only a small group whose characteristics enable them to dominate a community, perhaps by virtue of longer life, greater size or ability to withstand relatively large environmental variations. For example, the forest communities in the Basin are dominated by a small group of tree species (Table 1) that account for most of the stems and the bulk of the biomass. The tendency for a few species to be dominant makes the classification of communities possible.

Communities may be grouped in several ways: by general appearance and dominant life form, for example, as broadleaf or coniferous forest, grassland or shrub communities; by the dominant species such as the maple-beech forest, the bluestem prairie, tamarack swamp or sphagnum bog; or as functional entities, related to environmental parameters, such as lowland forest, pine barrens or wet prairie.

Table 1 lists importance values for major tree species found in northern and southern forest communities. The relationships between various communities can be determined by comparing species values; similar comparisons could be made for shrub species and herbaceous plants. The importance value is a composite measure including frequency of occurrence, basal area (size) and density (stems per unit area) for each species. These values are calculated for each species in a stand, totaled for all species, and the percentage of the stand total represented by each species is determined. The sum of the percentage frequency, basal area and density for each species is its importance value in that stand.

As with soils, the major vegetational continua are those related to available moisture or to growing season length and temperature. Thus there is a gradual transition in both forest and non-forest communities from north to south across the Basin (Figs. 2 and 3). The greatest variation appears within the area of sharpest climatic change, designated as the transition zone. As with soils, there are continua from wet to dry sites within the Basin.

The glacial topography of the Lake Michigan Basin makes the demonstration of continua relatively easy. Within a short distance one may move from a deep kettle in a moraine to a mesic north slope to a well drained outwash area of silty sand or to a dry gravel esker. Sometimes the transition between adjoining communities is abrupt, as for example, when a coarse sandy outwash supporting northern xeric forest adjoins a recessional moraine supporting northern mesic forest or a sphagnum bog on peat. More often, however, the transition between communities is gradual. Continua are evident on both the micro- and macro-scale. A wide belt of transitional forest may lie between the lowland forest and the upland mesic community or between prairie and southern mesic forest. On the other hand, small differences in topography, drainage or soil texture may produce habitats within any community which support, on a few square meters, a community different in composition from that on the surrounding land. Communities forming the continuum need not be adjacent to each other since the continuum is based on species composition as it has developed under the constraints of climate, chance and soils.

In the preceding discussion, forest, grassland, shrub and wetland communities have been described in some detail. Several other recognizable biotic communities occur in limited areas in the Basin; these include: bracken grassland, fen, cedar glade, sphagnum bog and communities of submerged and emergent aquatics. Descriptions of these communities may be found in Curtis (1959).

Species	Boreal	Wet	Wet Mesic	Mesic	Dry Mesic	Dry	Pine Barren
Northern Forest Communities							
Sugar maple *Acer saccharum*				107	27		
Beech *Fagus grandifolia*				40			
Hemlock *Tsuga canadensis*			40	79			
Yellow birch *Betula lutea*			34	29			
Basswood *Tilia americana*				16			
Balsam fir *Abies balsamea*	70	24	45				
White cedar *Thuja occidentalis*	32	45	91				
White spruce *Picea glauca*	25						
Black ash *Fraxinus nigra*			27				
Red maple *Acer rubrum*					37		
Red oak *Quercus borealis*					36		
White pine *Pinus strobus*	34				75	43	
White birch *Betula papyrifera*	26				30		
Red pine *Pinus resinosa*						48	8
Hill's oak *Quercus ellipsoidalis*						37	58
Bur oak *Quercus macrocarpa*							28
Trembling aspen *Populus tremuloides*						21	
Big toothed aspen *Populus grandidentata*							10
Jack pine *Pinus banksiana*		14				65	187
Tamarack *Larix laricina*		56					
Black spruce *Picea mariana*		139					
Climate and Soil							
Total precipitation, inches	26.8	31.0	31.0	30.8	30.0	30.0	28.6
Snowfall, inches	53.8	50.9	50.9	52.1	49.6	49.6	48.3
Growing season, days	137	136	136	127	123	123	118
Soil pH	5.1	4.7	5.5	5.6	5.2	4.9	5.2
Water-retaining capacity, %	225	670	495	250	130	120	36

Table 1. Continued

Species	Wet	Wet Mesic	Mesic	Dry Mesic	Dry	Oak Opening
Southern Forest Communities						
Sugar maple *Acer saccharum*			126			
Beech *Fagus grandifolia*			30	23		
Slippery elm *Ulmus rubra*			26	17		
American elm *Ulmus americana*	27	74				
Basswood *Tilia americana*		24	34	29		
Red oak *Quercus borealis*			21	104	22	
Shagbark hickory *Carya ovata*						20
White oak *Quercus alba*				52	80	62
Black cherry *Prunus serotina*					23	
Black oak *Quercus velutina*					98	72
Bur oak *Quercus macrocarpa*					26	105
Hill's oak *Quercus ellipsoidalis*						9
Black willow *Salix nigra*	64					
Cottonwood *Populus deltoides*	55					
River birch *Betula nigra*	24					
Silver maple *Acer saccharinum*	82	58				
Green ash *Fraxinus pennsylvanica*		27				
Black ash *Fraxinus nigra*		16				
Climate and Soil						
Total precipitation, inches	31.5	31.5	30.6	30.6	30.6	31.6
Snowfall, inches	41.9	41.9	45.8	42.5	42.5	43.1
Growing season, days	151	151	154	137	137	145
Soil pH	7.0	6.1	6.9	6.4	6.2	6.5
Water-retaining capacity, %	62	118	75	86	73	83

[a]Data from Curtis, 1959.

PART 2. PRESENT PLANT COMMUNITIES

INTRODUCTION

The major plant communities that occupied the Basin at the time of settlement were described in the preceding section. Glacial and postglacial history had much to do with their composition, and especially with the pattern in which they were distributed. These natural communities were well adapted to the diverse combinations of climate and soils resulting from glacial action.

In contrast, the structure and distribution of the present plant communities have been profoundly affected by the disturbances associated with European settlement.

The settler's needs for lumber, food, and fuel resulted in the disruption and replacement of the natural communities. Lumber production for export also led to major changes.

In the early decades, dependence on water transportation concentrated settlement where river mouths and bays provided harbor facilities. Today, few if any, intact marshes remain in the bays or at river mouths around Lake Michigan.

Agriculture began early in the southeastern corner of the Basin where settlement was rapid. Settlers reached Indiana from the south and east and soon pushed northward into southern Michigan, joining those who entered Michigan by the Lake Erie route. By the time of Michigan statehood (1837), that state's agricultural economy was well developed. Poor river transportation (Michigan rivers were shallow with many obstructions) forced early development of roads and railroads both westward and northward, aiding the spread of agriculture (Hudgins, 1948). In Wisconsin and Illinois, agricultural development began near the coastal towns and spread rapidly into the fertile lands of the Basin along the western shore of Lake Michigan.

Farming began in forested areas near the growing settlements. Increased demand for food stimulated technological advances which allowed the farmers to move onto the open oak savanna and the fertile prairie lands. Today, the prairies have been largely replaced by cultivated crops or pasture. In Illinois and Wisconsin, agricultural development diminished and eventually eliminated the prairie fires and permitted the oak openings and savannas to develop into oak forest.

The oak forests of southern and western Michigan, northern Indiana, and southern and eastern Wisconsin provided building material and fuel. Many stands of oak were logged; most others were grazed heavily. Continuous grazing by cattle or horses caused profound modifications in forest structure and reproduction.

Demand for timber and fuel also affected the beech-maple forests and the conifer swamps of Indiana and lower Michigan; tamarack was a good barntimber. After logging, the conifer swamps were converted to marsh. The enlarged marshes were pastured, were often mowed for hay, or reverted gradually to shrub-carr communities of red osier dogwood, willow, and poison sumach. In dry years, fire played a part in these conversions. Extensive development of lowland hardwood forest may have been aided oy human intervention, i.e., by stopping the burning of the meadow and shrub communities.

As lumber needs accelerated, so did the pace of logging; the peak of timber production in lower Michigan occurred about 1880 to 1890, in Wisconsin near 1900, and in the Upper Peninsula of Michigan a few years later. Logging had several effects. A light cut would hasten the transition from a shade-intolerant forest community towards one of more shade-tolerant species. Sugar maple or beech, for example (often already present under a pine or oak canopy), more shade-tolerant and in closer tune with the climate, were often favored. In contrast, heavy logging would generally set back the developmental process and favor pioneer communities of pine or aspen.

Increased logging and settlement resulted in increased frequency of fires. Hot fires, feeding on the dry slashings, often eliminated seed sources, inhibiting regrowth of the logged forest. On occasion, recurrent fires (largely of human origin) even eliminated or severely restricted the development of the pioneer aspen and birch communities, and produced large areas of grassland, previously rare or absent in the north.

Most of the original forest communities in the Basin have been altered in species composition, structure, and age distribution. However, with some exceptions, the descriptions of the presettlement forests hold reasonably well for the present disturbed and younger representatives of those same communities. In some cases, for example, the spruce-fir forest, fire control may now be permitting expansion of the acreage occupied.

Large areas of cutover forest land were slow to regain tree cover but today these areas are either covered with aspen-birch or are developing into other forest similar to that which once covered the land.

In the agricultural regions of the Basin, settlement and cropping patterns became the predominant influences on the natural communities. Preservation of a "back-forty" farm woodlot depended upon cultural factors, economics, need for fuel, and the nature of the land occupied by the original forest.

Tradition has much to do with farm patterns. Those areas in which woodlots were useful, desired, or well protected by rough terrain or poor drainage, usually remain in forest today.

Cultivation, logging, and other disturbance opened the soil for invasion by vigorous and aggressive plants, many of which had evolved under European agricultural conditions. Spreading by wind, contamination of crop seed, shipment of hay and feed, and movement of man, animals, and harvested grain, weed species rapidly colonized basin soils. Sorted by soil conditions and climate, weed communities have evolved north as well as south of the tension zone, each cropping pattern has its particular weed associates.

Agricultural technology also played a large part in determining present communities. The advent of the tractor, bulldozer, and similar machinery permitted cultivation of ground previously difficult to farm; terracing did not open up the sloping land, although it helped to preserve its value as farm land. The greatest impact has occurred in the last several decades. Increasing mechanization of farms has made production volume a critical factor in economic success; "clean" farming, augmented by tile drainage, has eliminated fencerows, ditches, and often the entire farm woodlot as well. The tractor also increased the ability of a single farmer to crop a larger acreage, thus encouraging land clearing on the home farm.

Vegetation units today show a greater degree of interspersion as compared to the presettlement pattern. The fine patchwork mosaic includes both independent, naturally evolved communities and those man-dominated agricultural and urban ones.

A brief account of the present biota of the Basin is presented in the following pages. The Basin is divided into five geographical regions and land use changes in these regions are discussed. Selected important agricultural communities are described. Illustrative summaries of vegetation of nine counties are appended (Appendix B) to give a microlevel picture of the present biotic diversification. The aspen-birch forest community, which has expanded greatly since settlement, is discussed in detail.

VEGETATION REGIONS IN THE BASIN

SOUTHERN AND SOUTHWESTERN FRINGE--Indiana, Illinois, and Southeastern Wisconsin

This relatively small area, once largely prairie, dune, and wetland, is now heavily populated, industrialized, and largely urban, with only limited remnants of the original communities. Agricultural use persists, especially in southeastern Wisconsin, although the better soils are often preempted for urban uses.

EASTERN AGRICULTURAL AREA--Northeastern Indiana and Southwestern Michigan

A glaciated area of level to rolling topography, this was once covered largely by oak-hickory (dry mesic) forest with maple-beech (southern mesic) forest on the more fertile soils, lowland forest and sedge meadow on the wetter soils, and with a few patches of prairie. Now, the area is predominantly agricultural, with the exception of meadow, shrub-carr, and lowland forest on poorly drained soils, and occasional woodlots of maple-beech or of oak. Crops are diverse, ranging from field corn and pasture to truck crops and mint. The counties along Lake Michigan are major fruit producers. Urban aggregations (e.g., Grand Rapids, Lansing, East Lansing, and South Bend) occupy sizable areas.

NORTHWESTERN LOWER PENINSULA AND LAKE SHORE REGION

The northwestern portion of lower Michigan, including a strip extending down the eastern shore to Muskegon, was once largely pine (northern xeric)

forest on the outwash sands and maple-beech (southern mesic) forest on the moraines. The usual intermixture of lowland forest and bog was present. The area is now covered by second-growth forests of oak and pine, pine plantations, aspen-birch stands, and pole-sized hardwoods. A major fruit-growing area extends north along the shoreline. Limited urban concentrations occur from Muskegon northward.

NORTHWESTERN REGION--Eastern and West Central Part of Michigan's Upper Peninsula and Northeastern Wisconsin

This region of relatively level terrain with generally infertile soils originally supported northern swamp-conifer on the poorly-drained sites, intermixed with pine or maple-beech on the better-drained sites. A few areas supported boreal (spruce-fir) forest. The vegetation is now largely second-growth forest, chiefly aspen-birch, pine, or swamp-conifer with some second-growth sugar maple or northern mesic forest. At the most western edge of the Basin, heavier soils support vigorous second-growth stands of northern mesic forest. Neither agriculture nor urban uses occupy appreciable areas, save near Lake Michigan. Agricultural use is limited chiefly to potatoes, small grains, and dairy cattle. Urbanization along the shoreline began as centers for the logging industry and remains limited.

EAST-CENTRAL WISCONSIN AND DOOR COUNTY

The Door County Peninsula and the adjoining northern counties were once northern mesic or conifer forest, while to the west and north of Lake Winnebago, oak savanna dominated. Maple-beech (southern mesic) forest was common south and east of Lake Winnebago. An intensive agricultural economy of diverse crops, including corn, peas, oats, soybeans and alfalfa, has replaced the natural vegetation. Dairying is a major farm activity and Door County has extensive apple and cherry orchards.

Urbanization has been extensive, extending from Milwaukee to Green Bay and on the south, west and north shores of Lake Winnebago.

AGRICULTURAL COMMUNITIES

Generally, the virgin soils stripped of forest by the pioneers were rich in humus and nutrients and produced good crop yields. The farmers selected species which grew well and produced the largest yields possible under the restrictions of the climate, length of growing season, and soil conditions. However, annual plowing and harvesting reduced natural soil fertility and promoted erosion of the topsoil. Yields diminished as the lush growth obtained during the early years of agriculture declined. If yields were to be maintained and increased, added nutrients were needed, at first, barnyard manure and later commercial fertilizers were applied in an attempt to supplement nutrient supplies for the plants. In addition, crops were selected for high yield, disease resistance, and climatic adaption. As elsewhere, technology was called upon to produce insecticides and herbicides to combat the insect and disease problems characteristic of the vulnerable, single-species crop system. Irrigation and drainage systems were developed to ease some of the limitations on land in agricultural use.

Some areas, not suited for farming, failed to respond to modern agricultural practices. Warm season crops, notably corn, were failures in the north where the short growing season is frequently interrupted by summer frost. The level, sandy outwash plains, although easy to till, were low in soil fertility and subject to summer drought. These areas were adapted only to hay or pasture production (and in some areas potato growing), while long winters made dairy farming difficult and costly.

Other lands proved too rocky even for pasture, and when the post-logging wave of farmers experienced frustration and failure, many farms were abandoned or were converted to hay or small dairy operations. In recent decades, much of this abandoned land has been replanted to trees, for cellulose or Christmas tree production.

The agricultural landscape evolved into a highly specialized system. Enormous quantities of fossil fuels, nutrients, and biocides are required to cope with the demand placed on the system. Soil depletion and erosion are major problems in many areas of the Basin. New problems involving biological food chains have been created by the use of insecticides and herbicides. Human population growth requiring food and space constantly strains the already fragile structure of this system.

The ensuing discussion highlights some of the cropping done under agricultural practices in the Basin. General distribution of Basin crops is also outlined in the discussion. Acreage of the major crops is given by counties in Table 2.

FIELD CROPS

Field crops are grown chiefly in the southern portions of the Lake Michigan Basin. Climatic conditions do not favor the growth of field crops in the northern part of the Basin. Even in southern Michigan or Wisconsin, climate often imperils agricultural prosperity. Modern machinery and special crop varieties have overcome some of the problems.

Wisconsin is known for the intensive agriculture of the southern, eastern and southeastern counties. In 1969, the state was first in the nation in production of corn for silage (10.9% of the national production), hay (8.6% of the national production) and green peas for processing (25.6% of the national production) (WSRS, 1970).

Corn grown for grain is usually planted in May and harvested in October or November, and corn for silage is harvested in September. In Indiana, corn fields may be planted at a density as great as 20,000 plants per acre (Kohnke and Robertson, 1966).

Oats are often planted as a nurse crop for hay; planting is usually completed in early May. Oats are harvested in July or August, and the straw is baled and used as bedding.

Wheat is generally raised as a cash crop. Winter or spring wheat is grown for harvest in July or August. At one time wheat was a much more important crop in the Basin; an infestation of cinch bug eliminated it as a major crop.

Table 2.   Acreage of Major Crops in Lake Michigan Basin Counties (1969)

	Corn for Grain	Oats	All Hay[a]	Soybeans
Wisconsin				
Brown	6,000	47,300	86,800	100
Calumet	11,700	28,800	58,500	450
Door	1,000	31,700	49,200	50
Florence	0	1,100	6,200	0
Fond du Lac	47,200	57,100	83,200	3,400
Forest	0	1,700	9,100	0
Green Lake	31,400	16,900	24,200	450
Kenosha	21,100	8,600	17,900	9,100
Kewaunee	2,100	36,000	58,600	50
Langlade	200	18,000	28,700	0
Manitowoc	10,700	56,500	92,900	300
Marinette	4,000	14,500	37,300	0
Marquette	13,300	7,200	25,200	400
Milwaukee	2,900	1,300	3,200	1,650
Oconto	9,800	27,100	55,900	100
Outagamie	29,400	39,600	82,500	1,150
Ozaukee	10,600	14,500	24,300	500
Racine	25,200	11,800	19,600	15,800
Shawano	10,000	38,600	91,400	100
Sheboygan	14,000	39,700	72,400	200
Walworth	74,400	22,300	44,300	9,700
Washington	17,800	28,000	46,500	450
Waukesha	21,000	14,000	39,400	4,200
Waupaca	14,700	27,700	61,500	200
Waushara	18,100	10,500	32,900	1,300
Winnebago	25,900	28,800	50,600	6,800
Upper Peninsula of Michigan				
Delta	0	6,500	16,000	0
Dickinson	0	1,500	5,000	0
Iron	0	1,000	6,500	0
Mackinac	0	2,500	5,000	0
Menominee	0	10,500	37,000	0
Schoolcraft	0	0	2,000	0
Lower Peninsula of Michigan				
Allegan	40,600	9,500	32,000	0
Antrim	0	2,000	10,500	0
Barry	23,600	9,500	30,000	1,500
Benzie	0	0	1,500	0
Berrien	23,900	3,500	8,000	17,000
Branch	47,300	6,500	17,000	24,000
Calhoun	47,500	12,000	28,000	6,000
Cass	38,900	6,500	13,000	18,500
Charlevoix	0	1,500	13,000	0
Clinton	42,700	10,000	35,000	25,000

Table 2. Continued

	Corn for Grain	Oats	All Hay[a]	Soybeans
Lower Peninsula of Michigan				
Eaton	34,000	8,000	31,000	4,000
Emmet	0	2,500	15,000	0
Grand Traverse	2,100	1,000	8,000	0
Hillsdale	44,500	10,500	30,000	25,000
Ingham	35,700	6,500	30,000	6,000
Ionia	38,300	13,000	31,000	2,500
Jackson	33,500	7,000	29,000	2,000
Kalamazoo	27,400	10,000	12,000	2,900
Kalkaska	0	0	2,500	0
Kent	26,700	9,500	37,000	0
Lake	0	0	6,000	0
Leelanau	0	1,000	7,000	0
Manistee	0	0	7,000	0
Mason	5,100	3,500	18,000	0
Mecosta	8,800	3,000	21,000	0
Missaukee	3,000	3,500	24,000	0
Montcalm	22,300	8,500	27,000	1,400
Muskegon	5,800	2,000	12,000	0
Newaygo	10,400	4,000	23,000	0
Oceana	4,900	2,000	16,000	0
Osceola	0	3,000	28,000	0
Ottawa	24,300	7,000	30,000	0
Roscommon	0	0	1,500	0
St. Joseph	36,100	6,000	16,000	26,000
Shiawassee	31,300	15,000	23,000	40,000
Van Buren	27,600	4,000	18,000	1,000
Wexford	0	0	6,500	0
Indiana				
Elkhart	60,500	8,000	21,700	32,200
Lake	55,500	6,600	9,200	32,200
La Grange	42,400	9,200	25,900	13,400
La Porte	77,800	4,000	13,400	54,500
Noble	50,600	9,300	22,800	24,300
Porter	55,800	6,500	9,300	37,600
St. Joseph	52,800	2,500	10,100	38,300
Steuben	28,400	5,700	17,500	12,000

[a] *Hay includes alfalfa, timothy-clover and other combinations reported by Wisconsin and Michigan (WSRS, 1970; Michigan Department of Agriculture, 1972).*

Red clover is well suited for a short rotation with grains in most areas of the Basin; it quickly enriches the soil with nitrogen and is a short-lived perennial which does not persist as the crop is changed.

Soybean acreages have increased greatly since 1930. Fields are plowed in fall or spring, the seedbed is prepared in May, summer cultivation is routine, and soybeans are harvested in fall.

HAY LAND

The crops produced and the associated agricultural practices in the Basin are geared strongly to dairy farming. Dairy cattle require feed high in protein. Legumes, when grown in mixtures with bromegrass and timothy, provide such a suitable diet. Alfalfa and red clover are the legumes most often grown in the Basin; Wisconsin, Michigan, and Illinois are among the top ten states producing these crops (Smith, 1960; WSRS, 1970). Alfalfa normally produces more forage of higher quality than clover or timothy, and is more effective in controlling erosion.

The shorter growing season, cooler climate and lower proportion of precipitation received during the growing season make northern Wisconsin, the Upper Peninsula, and the northern portion of the Lower Peninsula better suited for growing forages than for field crops. However, forage crops are grown throughout the Lake Michigan Basin.

Forage crops are generally sown in the spring, often with a nurse crop of oats or barley. The first cutting is taken the following year. Most of the crop is harvested for hay, but some is harvested for silage.

Agricultural varieties of alfalfa produce two to three stands per growing season. The optimum time to cut each stand is determined by the stage in development, which can vary by several weeks from year to year due to climatic variations, rather than by a calendar date. If cut too early, energy reserves in the roots are not sufficient for regrowth and the next stand will give poor yields (Smith, 1960).

In most counties of the Lake Michigan Drainage Basin, red clover (*Trifolium pratense*) is second only to alfalfa in acreage planted and yields obtained. Red clover is usually grown with timothy, and crop-reporting services usually lump the result as timothy-clover hay.

Red clover is commonly seeded with a nurse crop, usually oats, to prevent early maturity and flowering. Plants which flower during their seedling year are more susceptible to winter killing and produce smaller yields the following year than those which do not flower (Bird, 1948; Smith, 1957; Therrien and Smith, 1960). After the oats are harvested, a still greater yield increase can be obtained in the following year if the clover is mowed (Klebesadel and Smith, 1958; Therrien and Smith, 1960).

Moderate climate, fertile and well-drained soils, and abundant rainfall are required to obtain good clover yields. Even under optimum conditions, clover yields less, is more drought-susceptible and is less winter-hardy than alfalfa. Red clover is weakened seriously at high temperatures (95°F) and by low soil moisture (Kendall, 1958).

Like alfalfa, red clover produces several spurts of growth annually; three crops during the growing season can be normally expected.

The first cutting of red clover produces the highest quality seed and largest hay yield. Seed, however, is usually obtained from the second cutting rather than the first because cattle feed has a higher priority.

PASTURE

Pasturing is one of several agricultural systems which converts vegetation to beef and dairy products. However, it is still a subsidized system requiring human energy for maintenance through fertilization, application of herbicides and insecticides for weed and insect control, selective breeding of pasture species, irrigation, and grazing management.

In the Lake Michigan Basin, possibly 80% of the pastures are used for dairy operations. These pastures are composed of combinations of tall and low grazing species of grasses (brome grass, orchard grass, Kentucky bluegrass, Canada bluegrass, timothy, and reed canary grass) and legumes (such as alfalfa, and red and white clover) which harbor the bacteria essential to fix atmospheric nitrogen. The highly palatable legumes thus increase plant nutrient supply resulting in improved grass yields. Alfalfa is usually used for pasture in preference to clover because although clover produces a good crop the year after planting, it declines rapidly thereafter. Weedy plants are usually present in pastures, including some often unpalatable or sometimes poisonous species (e.g., elderberry, Canada thistle, white snake root, stinging nettle, and goldenrod). In old or poorly managed pastures, less productive grasses, such as Junegrass or quackgrass, often replace the productive and more nutritious forage plants. Palatability and the amount and types of proteins, vitamins, and minerals vary with the species of plants grown, their stage of growth, and the total growth. Grazing and midsummer drought affect growth.

Pasture can be classified as rotation, permanent, or supplementary (Smith, 1960). Rotation pasture occurs mostly on level terrain and involves alternation of pasture with a row crop such as corn or oats, or with hay production for silage and green chopping. Rotation pastures are managed for species mixes which promise high yields (e.g., alfalfa-brome grass, alfalfa-brome grass-clover, or orchard grass-clover). These legume-grass mixture pastures are established on well drained soils (Tesar and Hildebrand, 1966). In contrast, permanent pastures are allowed to build a thick sod layer; such areas include bluegrass and low wetland pastures (reed canary grass). Reed canary grass is a coarse, leafy, long-leaved perennial which thrives on muck soils (Harrison and Davis, 1966). Thus lowland areas are often occupied by reed canary grass and provide a valuable source of pasture during summer months of scarcity. Supplementary pastures are those used when other pasturage is depleted or inadequate in amount, and areas are sometimes intentionally planted for this use. Sudan grass, spring and winter wheats, oats, rye and sweet clover, or hay fields which have been mowed for the last time, may all be used for supplementary pastures.

Pastures are continuously consumed by cattle grazing and, to a small extent, by insects and diseases. They require close management to maintain vigorous growth and dominance of the palatable species. Tons of lime, manure, and commercial fertilizers high in phosphorous and potassium must be supplied

yearly to maintain large yields and desired composition. Legumes grow most successfully in sweet (neutral) soils. Selective breeding has produced high-yielding grasses and legumes well adapted to the specialized, often harsh pasture environment.

Although man-made and relatively simple in structure, pastures may display successional trends similar to natural communities; these trends result from changes brought about by grazing. With light continuous grazing, tall upright species such as Canada bluegrass, timothy, and orchard grass may dominate over the lower growing Kentucky bluegrass and white clover, and weeds do not invade readily. Moderately heavy or heavy continuous grazing may permit low-growing species to dominate, although weeds may invade. Heavy continuous grazing reduces the tall-growing less desirable grasses and weeds which are palatable when young. Overgrazing results in weak plants, thin sods, lowered productivity, and an increase in weeds. With heavy alternate grazing (discontinuous use), tall- and short-growing species and weeds do well (Smith, 1960).

Alfalfa and other legumes essential for dairy cattle can be maintained in pasture most readily under rotational grazing. In general, a dairy farm as compared to a farm raising beef cattle sustains heavier pasture grazing, has a smaller percentage of pasture, more often requires supplementary pastures, and has considerable acreages of legumes for hay (Smith, 1960).

Type and length of pregrazing period will also influence pasture composition and species dominance. Many species are prevalent because they are inedible or unpalatable. Other species cannot survive the constant disturbance. Forage waste from trampling and manure may exceed 20 to 30 % of total growth (Smith, 1960).

FRUIT AND VEGETABLE CROPS

Appreciable acreages of fruit and vegetables are sound throughout the Basin. Fruit production is concentrated in Michigan's shoreline counties and on the Door County Peninsula in Wisconsin. Door County is the major apple- and cherry-producing county in Wisconsin; some apple orchards are found in the counties along the lake south of Green Bay and also in Waupaca County to the west. A small part of Wisconsin's sizable cranberry crop is grown in the northwestern edge of the Basin.

Michigan is the leading deciduous (non-citrus) fruit-producing state east of the Pacific Coast states, and in volume of production and diversity of crops, ranks among the top five states in ten important fruits: apples (third), peaches, tart cherries (first), sweet cherries, plums (second), grapes, blueberries, strawberries, and raspberries (in top five) (Hull, 1970; Hull *et al.*, 1973; Johnston and Moulton, 1968; Johnston *et al.*, 1969).

The distribution, yields, and environmental requirements for major fruit crops are shown for Michigan in Table 3.

Vegetable crops occupy major areas in the Lake Michigan Basin as well as the adjoining areas outside the Basin. The important vegetable crops in the Basin include sweet corn, beans, peas and potatoes in Wisconsin and asparagus, celery, onions, potatoes, carrots, cucumbers, melons (muskmelon and watermelon), and tomatoes in Michigan. With the exception of sweet corn, beans, tomatoes,

Table 3. Fruit Production in the Lake Michigan Basin Portion of Michigan[a]

Crop	Area of Major Production	Climatic Requirements	Soil Requirements	Average Annual Production
Apples	Southwestern and west-central Michigan north to Cheybogan County.	Cool to moderate temperatures without late spring frost.	Wide range of soils.	6.4 tons/acre
Pears	Berrien, Allegan, Van Buren, Mason, Oceana, and Kent counties.	Cool temperatures with good air drainage.	Well-drained silt loams or clay loams with sandy to clay loam subsoil.	2.3 tons/acre
Peaches	Allegan, Van Buren, Berrien and Oceana counties.	Cool to moderate temperatures moderated against late frosts and extreme winter temperatures.	Light, well-drained soils.	3.3 tons/acre
Tart cherry Sweet cherry	Western Michigan near the lake.	Cool to moderate temperatures with protection from late frost.		2.4 tons/acre 2.0 tons/acre
Plum	Berrien and Van Buren counties. Some grown in north-central and north-eastern counties along Lake Michigan.			2.5 tons/acre
Grapes	Berrien and Van Buren counties.			3.4 tons/acre
Highbush blueberry	Berrien, Van Buren, Allegan, Ottawa, and Muskegon counties.	Moderate winter and cool extended growing season.	Low, moist, acid soils.	4-7000 pints/ acre
Strawberry	Berrien, Van Buren, Manistee, and Leelanau counties.	Cool areas where frosts are moderated.	Well-drained soils high in organic matter.	4,633 lb/acre

[a]Hull, et al., 1973.

and melons, the list includes crops best suited to cool and moderate temperatures and adapted to sandy or muck soils. The melon and tomato acreages in the Basin are found chiefly in Berrien and Van Buren counties, Michigan, and sweet corn in southeastern Wisconsin.

Suitable soil conditions, moderately cool growing seasons, and increased irrigation to supplement rainfall all favor potatoes as the major crop in the northern and central parts of the Basin.

Potatoes grow best on well-drained and well-aerated sandy, peat, or muck soils which allow for growth of a well-shaped tuber and for easy tilling and harvesting. The potato is best adapted to average day temperatures below 70°F and cool nights are essential for carbohydrate accumulation in the tubers (Chase and Thompson, 1967).

FOREST COMMUNITIES

The present forest cover in the Basin is well documented and its distribution mapped (Fig. 6). At intervals of approximately ten years, a forest survey is conducted cooperatively by the state and the U. S. Forest Service (Chase, Pfeifer and Spencer, 1970; Spencer and Thorne, 1972; Spencer, 1969; and Essex and Gansner, 1965).

The forest survey data aggregate forest vegetation into six major types, as indicated below:

Major Forest Types (Cooperative Forest Survey)	Corresponding Natural Communities (Curtis, 1959)
White-red-jack pine	Northern xeric forest
Spruce-fir	Boreal or northern lowland forest
Maple-beech-birch	Northern or southern mesic forest
Oak-hickory	Southern xeric forest
Elm-ash-cottonwood	Southern lowland forest
Aspen-birch	Successional forest

These first five represent original forest communities and were described earlier. Descriptions of the now widespread aspen and aspen-birch communities are provided here. The effects of human disturbance on these forests as well as on other native vegetation will be described in more detail in Part 3 on community dynamics, while the productivities of the major vegetation types are discussed elsewhere in the series.

The total commercial forest area in the Basin is approximately 10,743,790 acres, of which 5,096,615 lie in lower Michigan, 1,842,275 in the Upper Peninsula of Michigan, 3,580,500 in Wisconsin, and 224,400 in Indiana. Table 4 gives the acreages of major forest types in the Lake Michigan Basin counties.
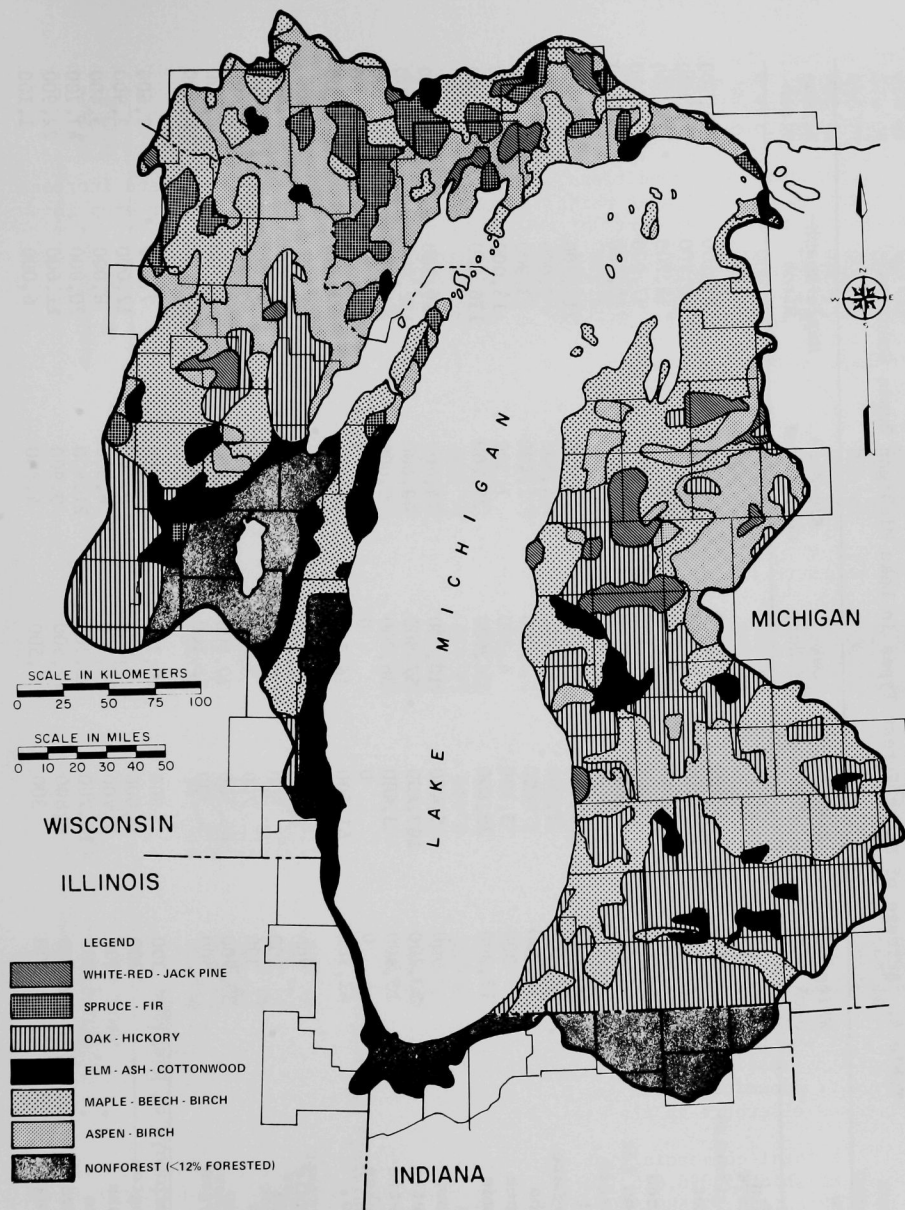
Fig. 6. Distribution of Present Forest Communities. Compiled from U. S. Forest Service reports, Michigan (Chase, Pfeifer and Spencer; 1970), Wisconsin (Spencer and Thorne; 1972).

Table 4. Acreage of Major Forest Types in Lake Michigan Basin Counties[a]

	White-Red-Jack Pine	Spruce-Fir	Oak-Hickory	Elm-Ash-Cottonwood	Maple-Beech-Birch	Aspen-Birch
Wisconsin						
Brown	300	3,200	4,400	9,600	15,100	3,500
Calumet	300	1,300	7,100	6,700	6,700	2,800
Door	500	19,600	6,000	13,700	32,200	21,300
Florence	18,300	33,500	14,100	9,800	97,000	86,000
Fond du Lac	1,100	2,700	14,100	11,900	10,100	6,800
Forest	27,400	108,400	7,700	16,900	218,300	139,200
Green Lake	200	1,500	11,200	4,300	7,000	2,500
Kenosha	300	400	2,400	1,400	3,900	1,200
Kewaunee	300	3,300	4,300	7,300	13,000	2,600
Langlade	17,900	75,800	16,600	25,200	116,400	126,100
Manitowoc	900	5,400	10,900	14,400	19,300	7,500
Marinette	53,100	103,400	57,900	49,600	132,800	243,300
Marquette	15,400	3,400	36,700	9,000	9,500	21,100
Milwaukee	0	0	0	0	0	0
Oconto	41,700	61,500	16,500	39,200	83,300	108,000
Outagamie	700	4,600	12,000	21,800	17,300	8,800
Ozaukee	100	600	4,200	2,200	3,200	3,500
Racine	300	700	3,000	2,500	5,600	2,600
Shawano	37,900	66,500	30,500	39,900	168,900	138,700
Sheboygan	500	4,700	12,100	7,400	13,000	8,500
Walworth	300	800	10,200	4,200	7,000	2,600
Washington	200	2,000	8,000	9,400	12,000	2,900
Waukesha	200	2,700	20,900	6,500	8,000	5,400
Waupaca	16,300	10,200	38,300	21,400	20,900	47,700
Waushara	22,900	3,800	42,500	9,900	11,600	22,900
Winnebago	300	300	7,500	4,800	6,000	1,100

Table 4. Continued

	White-Red- Jack Pine	Spruce- Fir	Oak- Hickory	Elm-Ash- Cottonwood	Maple-Beech- Birch	Aspen- Birch
Upper Peninsula of Michigan						
Delta	90,100	178,600	3,200	46,300	139,600	166,100
Dickinson	29,700	126,400	6,100	21,700	104,600	159,200
Iron	24,900	160,900	6,500	26,200	285,100	192,500
Mackinac	48,400	159,900	3,000	38,900	155,000	165,700
Menominee	23,700	191,400	4,800	50,100	134,800	108,500
Schoolcraft	83,900	178,700	2,000	67,200	179,800	119,800
Lower Peninsula of Michigan						
Allegan	7,500	1,900	55,800	35,900	30,300	18,700
Antrim	25,500	10,800	31,800	12,000	50,400	55,100
Barry	3,200	1,700	40,100	23,000	14,500	11,100
Benzie	9,600	8,400	14,400	15,200	37,200	37,200
Berrien	900	1,100	27,100	18,300	13,400	8,600
Branch	1,500	1,000	22,000	14,600	9,500	7,800
Calhoun	2,100	2,400	35,400	31,300	13,900	13,900
Cass	1,900	1,100	28,100	16,100	13,800	8,400
Charlevoix	5,300	14,500	16,700	11,400	63,700	50,100
Clinton	600	200	15,200	11,400	11,800	5,800
Eaton	1,400	900	13,400	14,700	15,300	10,100
Emmet	11,000	18,300	17,700	17,000	64,600	54,100
Grand Traverse	30,500	7,000	42,100	12,700	40,700	35,100
Hillsdale	1,100	1,100	28,400	18,200	12,500	8,700
Ingham	700	800	18,300	16,400	14,400	7,700
Ionia	1,700	500	18,600	14,600	17,400	10,600
Jackson	4,500	2,300	42,100	22,400	13,200	11,200
Kalamazoo	3,300	1,900	31,900	18,100	12,300	11,000
Kalkaska	72,400	29,600	43,100	18,300	53,900	53,400
Kent	7,800	1,900	42,700	30,200	27,300	18,800

Table 4. Continued

	White-Red-Jack Pine	Spruce-Fir	Oak-Hickory	Elm-Ash-Cottonwood	Maple-Beech-Birch	Aspen-Birch
Lower Peninsula of Michigan						
Lake	49,600	4,100	145,700	14,700	21,800	61,000
Leelanau	12,100	6,900	10,200	6,600	42,600	34,800
Manistee	26,900	6,300	66,200	15,500	41,100	64,200
Mason	24,500	3,000	51,600	9,400	31,400	38,700
Mecosta	9,700	5,700	32,300	12,800	32,600	55,300
Missaukee	11,100	34,500	17,500	17,300	57,500	89,200
Montcalm	8,500	2,300	46,100	33,400	24,600	18,800
Muskegon	10,100	1,700	82,300	29,000	27,100	18,800
Newaygo	29,900	12,900	93,100	31,300	47,200	95,800
Oceana	16,100	3,400	40,300	12,200	37,500	40,700
Osceola	11,200	8,200	20,100	17,800	47,700	69,700
Ottawa	12,600	1,300	39,700	14,400	13,200	7,200
Roscommon	37,300	40,600	67,700	23,800	29,100	71,400
St. Joseph	1,500	1,100	22,600	18,000	6,500	7,500
Shiawassee	800	100	13,500	10,200	12,700	5,200
Van Buren	3,400	2,000	29,700	30,800	19,300	14,400
Wexford	36,300	9,700	28,000	12,600	62,300	71,500

[a]Chase and Pfeifer (1969), Michigan Department of Natural Resources (unpublished), Pfeifer and Spencer (1969), Spencer and Pfeifer (1969), Wisconsin Department of Natural Resources (1968).

ASPEN AND ASPEN-BIRCH

In northern Michigan and Wisconsin, aspen and aspen-birch stands are the direct result of heavy logging followed by fire. In Wisconsin, the great explosion in aspen acreage occurred during the early 1900's (Fralish, 1972), and in Michigan, somewhat earlier (Graham, *et al*., 1963). For a period prior to 1950, aspen was considered economically unimportant, but the wood now commands a substantial market for pulp, plywood, composition board, and lumber for light framing and furniture (Garland, 1972; Keays, 1972). Aspen stands are also important to game managers, providing winter ruffed grouse food supplies and summer deer browse.

Today, in Wisconsin and Michigan, aspen stands cover approximately 8.5 million acres (Hansen and Kurmis, 1972); of this, 45 to 55% is in the Lake Michigan Basin.

The generic term aspen includes two species--trembling aspen and large-toothed aspen. The species differ somewhat in site requirements, with large-toothed aspen favoring more fertile and moist sites than trembling aspen. Clones of both species are often found in the same stand with balsam fir and hardwoods such as red maple and white birch.

Both aspens occur with birch on a variety of soil types and under various climatic conditions, but in the Basin they are most often found on sands or sandy loams in the north. Under favorable conditions, aspen grows rapidly, but in comparison to most forest trees, aspens are short-lived, deteriorate rapidly at maturity, and have high susceptibility to diseases and insects. In central Wisconsin, the maximum stand age may be between 25 to 35 years (Portage County), while 75 mi to the north (Lincoln County), it may be 45 to 50 years. In Sawyer County, 100 mi northwest of Lincoln County, the maximum stand age reached is about 55 to 60 years (Fralish, 1972).

A young aspen stand develops rapidly from root and stem suckers, and because it originated after fire or clearcutting, the stand is even-aged. Aspen is extremely intolerant of shade, and the dense growth shades out trees that are weaker or smaller. In healthy stands, dominant trees form a solid canopy, providing some mutual resistance to strong wind or heavy snow and sleet which can easily break branches or fell entire trees. As the stand reaches maturity, growth slows and individual stems die, commonly from the aspen canker, *Hypoxylon pruinatum*, or another fungus, *Fomes igniarius*, both of which weaken the stem, leaving it susceptible to wind damage (Anderson, 1972). Wind breakage and other mortality creates openings in the canopy which are not closed by the older, usually slower-growing trees. As the openings become frequent and larger, environmental stresses become greater. Other species may become established in the openings, depending on soil and climatic conditions, shade, and availabiliy of seed. The entire process of stand deterioration may take only three to four years (Fralish, 1972). Aspen stands may last only one generation if other species invade successfully.

The aspen stands originating in the 1900's are presently declining in area, not so much as a result of harvesting as of natural deterioration and natural conversion to northern hardwood or white pine. Complete conversion through natural succession has occurred in over 40% of the aspen-birch stands

in Wisconsin and upper Michigan (Heinselman, 1954). However, some new stands are being regenerated following the clear cutting of the mature aspen. New faster-growing varieties are being sought that also incorporate disease and insect resistance. Appropriate harvesting methods and intensive management are producing an increase in aspen timber volume, even though the total area under aspen forest is declining (McGuire, 1972). This increase may not fulfill future demands (Leuschner, 1972).

Aspen has a clonal growth form established by vegetative reproduction from root suckers and clones may be recognized by leaf morphology, seasonal coloring, stem form, branching habit, growth rate, and bark characteristics (Barnes, 1966). Stems of a single recognizable clone (i.e., a single individual) may cover from 0.05 to 35 acres (Blake, 1964; Barnes, 1966).

The extensive root network of aspen may produce a great number of suckers when the parent trees are cut and the forest floor receives sunlight; thus, aspen is easily regenerated (Farmer, 1962; Maini and Horton, 1966). Aspen suckers develop rapidly with nutrition obtained from the parent root and may grow four to five feet in their first year (Perala, 1972). The suckers are intolerant of shade and require full sunlight to develop sufficiently for rapid natural thinning and pruning. Young suckers produce adventitious roots which develop independently if the parent root system decays (Sandburg and Schneider, 1953). The adventitious roots of bigtooth aspen remain less important to the growth of the new stem than is the parent root until about age 25 (Zahner and De Byle, 1965).

White birch is the most common associate of aspen, especially following fire. Birch normally develops from windblown seed which germinates readily on exposed soil. Seedling growth is rapid and mixed stands of birch and aspen are widely dispersed. White birch also regenerates readily by stump sprouts. Birch is now being used extensively for wood pulp and often reaches greater size and age than does aspen. In many northern areas, red maple and balsam fir are common associates of aspen and may eventually become dominant in the stands. Beaked hazel is a common shrub and sometimes forms a dense understory. The aspen-birch community is extensive north of the tension zone in Michigan and Wisconsin and may develop in open areas, especially in burned lowland areas, in the southern part of the Basin.

CATTAIL INVASION OF DEPRESSIONS

In virtually every situation, the initial revegetation of a disturbed area is controlled by conditions affecting germination and seedling establishment, general availability of moisture, seed and suitable temperature. The cattail community is an excellent example of such a specific response.

The past decade has seen extensive disturbance of both native and cultural communities resulting from the construction of roads and highways and the development of subdivisions and various support facilities. Land grading is usually directed toward (1) leveling sloping land, (2) removing excess water ponded naturally in swamps and marshes or ponded artificially by construction, and (3) grading for road construction. In response to these manipulations, the cattail (*Typha* spp.) community appears as a frequent invader of roadside ditches, extensive swales, low scalped areas and in natural wetlands including northern lowland forests and sphagnum bogs where road construction has changed

drainage patterns. Observations in the Lake Michigan Basin suggest that wherever adequate moisture and fertility coincide, seed will become available (readily windblown) and a cattail stand may develop rapidly.

The cattail community may appear, at least for several years, as a pure stand in wetter portions of the depression or ditch. The edges of the depression are usually invaded by plants of the adjoining agricultural community, grasses, legumes and weedy species, by aggressive wetland forms as species of bulrush, bur reed and sedge (*Scirpus*, *Sparganium* and *Carex* spp.) and sooner or later by woody species. Cattails are vigorous plants capable of efficient production of organic matter as long as moisture and nutrients are available. They respond to nutrient additions and utilize effectively nutrients reaching them through runoff from adjoining or upstream fields. The cattail stand soon develops a dense subsurface mat. Organic matter accumulates rapidly from roots and rhizomes and from the dead and decaying tops. Where the stand is found in depressions with restricted outflow the ponded water helps to reduce decay and augment retention of organic matter.

The cattail community is also a conspicuous feature of streams and impoundments, especially in central and southern Wisconsin and in southern Michigan and Indiana. In these situations cattails, bulrush and similar species, often with clumps of willow, combine to form an exceedingly productive community covering large areas. Cattails in large stands are often attacked by stem borers or are utilized by muskrats and other wildlife; they may also be decimated when appreciable changes occur in water level (6 in. or more). In small stands they seem to thrive and appear to recover rapidly after being mowed or burned by surface fire, which, during the dormant season, may remove dead top material.

The cattail community, except in large marshes and lake borders, does not persist undisturbed for many years and is altered by invasion of other wetland species. However, the community is of widespread and frequent occurrence and lies at the critical interface between land and water. Since the cattail community has considerable importance wherever ponding and poor drainage occur, its presence should be considered relative to construction and maintenance activities for highways, impoundments and cooling ponds.

PART 3.   SUCCESSION IN PLANT COMMUNITIES

INTRODUCTION

If any one characteristic can be assigned to all biotic communities it is
that none is immutable. These communities continually undergo change; the
rate of change is highly variable, at times almost imperceptible and at other
times obvious to the least experienced.

A plant or animal population, whether of squirrels, June bugs, duck weed
or mushrooms, may change drastically in numbers from year to year; the
species composition and the dominant species may also change, although usually
much more slowly, but often measurably within a decade or two.

Community dynamics span several levels of magnitude in both time and
space. Changes, if caused internally, may be gradual and hidden, involving
the death or addition of a few individuals. In contrast, events (usually of
external origin) may cause widespread and unannounced fluctuations in single
species populations or in many populations in the community. Vagaries of
weather, heat waves, frosts, wind, ice or heavy rain, impacting suddenly or
unexpectedly are often responsible. Similar abrupt changes in animal popula-
tions parallel events in the plant community. If an acorn crop fails, the
squirrel population may be decimated through the following winter, a simple
and relatively obvious result. Less clearly known are the multitude of sec-
ondary interactions that may follow. Change may occur on a micro-scale stimu-
lated by as normal an event as the act of a black bear or a human entomologist
turning over a log, or a tree falling in a June storm. In contrast, triggered
by climatic catastrophe or fire, alteration of the plant community may involve
entire stands and may occur over extensive areas.

This section does not attempt a detailed discussion of the internal
fluctuations that occur almost routinely with little or no disruption in the
appearance and structure of the community. In this brief introduction to the
dynamic nature of community life, it is enough that the reader is aware that
natural and often quite large fluctuations occur in every living community.

Biotic communities usually start with colonization of bare soil, rock or
open water by individual species soon after the area is formed. The sequence
of processes in biotic communities, which result in recognizable alterations
in the composition and structure of the plant components, and of their animal
associates, is referred to as "succession." Primary (initial) plant community
development or succession follows a generally recognizable pattern which
starts with a fresh substrate and progresses to a stable or terminal community
adapted to the particular climate and region. This terminal community will
remain more or less unaltered in composition and function, save for minor
fluctuations, until it is perturbed by some major event.

Succession occurs in a directional fashion: a community is gradually
replaced by a better adapted and often more diverse one; the first plants to

be established flourish in full sunlight, they give way slowly to more shade tolerant species; plant biomass increases as does diversity in species composition. These trends are not inviolate; as the community approaches a steady state compositional diversity may again decline (Loucks, 1970). There is also a gradual change in the relative proportion of green plant producers and of animal and microbial consumers until, in the terminal stage, the utilization of stored energy (respiration and synthesis) essentially equals the rate of energy storage (photosynthesis).

For the sake of convenience, successional sequences are often classed in one of two groups: (a) those that originate when spores, seeds and other propagules are introduced into previously unvegetated substrates, such as beach sands, lakes, landfills or fresh rock surfaces (i.e., primary succession); and (b) those that develop after a disturbance, which may destroy the previous community without eliminating all propagules and surface organic matter present and sometimes even leaving a scattering of growing individuals (i.e., secondary succession).

The distinction between primary and secondary succession is arbitrary and there is no absolute difference between them. A diagrammatic view of the progressive changes which occur in a successional sequence appears in Figure 7 (McCormick, 1968). The secondary successions that follow a disturbance may be visualized as shown in Figure 7.
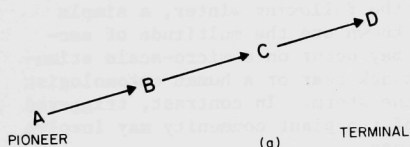
Fig. 7.
(a) Progressive Successional Change from Pioneer to Terminal Plant Community without Disturbance. Modified from McCormick (1968).
(b) Potential Pathway in Community Succession Following Catastrophe. The disturbed community may return to the original successional pattern through regression to an earlier stage, returning to the stage that suffered disturbance or, after minor disturbance, progression to a more advanced stage. Not all possibilities are shown since major perturbations, especially those caused by man, may preclude re-entry into the successional pattern.
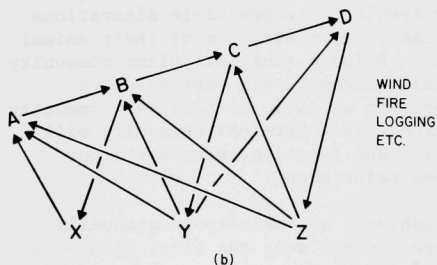
Basic concepts that emerge in any consideration of community succession include:

a. Small fluctuations in plant community structure are normally the result of the interaction of variations in climate with characteristics of the species present. A measure of community resilience is its ability to maintain recognizable composition and structure under environmental stress.

b. Communities not well adapted to a particular site and climate tend to be replaced by those better adapted, alterations in micro-climate and in soil caused by the existing community may be essential before a further change may occur.

c. Chance events must always be anticipated, they affect succession at all stages from initial vegetation development to establishment of the terminal community.

d. Succession involves both individuals and populations; both respond in considerable measure to the coincidence of natural events, especially the presence of propagules (seed, spores, sprouts, etc.) combined with favorable or unfavorable weather.

e. Community stability usually increases with successional development; the more complex the vegetational matrix the greater the number of alternative paths for recovery from perturbation and the more likely it is that the community will maintain itself. Native species are better tuned to local climate and hence are more capable of sustaining themselves under the range of climatic fluctuation within a region. At present, the temperature and precipitation regimes in the Lake Michigan Basin are those of a forest region which implies that forest stands will persist while hay fields or bluegrass lawns may soon change into brushy thickets and eventually succeed to forests.

f. Succession does not occur in cleancut and definite stages; each phase blends into the next. Since chance biological and climatic events are involved, it follows that the exact rate and direction of change is not completely predictable.

Development of succession theory received much support from early work done in the Basin; this work included the classic studies of the Lake Michigan dunes by H. C. Cowles (1901), of bog succession by Frank Gates (1942) and of forest development by W. S. Cooper (1913). In recent years, much additional knowledge has been gained concerning old field, prairie, and forest succession, bog and wetland development, beach and dune vegetation, and other matters pertaining to vegetation dynamics (Bray, 1956; Cottam, 1949; McIntosh, 1957; Olson, 1958; Stearns, 1949).

Plant succession also has practical implications for land management. Knowledge of succession and the reasons for change can help answer questions such as: How should power line rights-of-way be treated to maintain a stable low vegetation type at least cost? What management techniques are needed to maintain productive wetland? How can one maintain well-stocked aspen stands for pulp production?

SUCCESSION PATTERNS

The pages that follow describe some of the major patterns of change to be expected in representative situations in the Lake Michigan Basin. The discussions begin with primary succession from dune to forest and from lake to bog and then consider the complexity of vegetational change in the secondary successions which result from natural and human disturbance of native plant communities.

DUNE FORMATION AND SUCCESSION

Sand, from pulverized rock and wave erosion of glacial deposits, and calcium carbonates from crushed gastropod shells (Waterman, 1917) and other sources, are the medium upon which dune succession proceeds. Sand is deposited on the beach by high water currents and waves and carried across the land by wind. These particles catch and accumulate wherever vegetation, buildings or other stationary objects occur, forming dunes which in time may partially or completely bury the obstacles. Strength, frequency and direction of prevailing winds determine the particle size transported, speed of dune formation and dune shape, respectively. Once dune building has begun, most of the sand is deposited at the crest or on the lee side, resulting in a gentle windward slope and sharp drop on the lee slope.

Dunes continue to move until stabilized by mat forming vegetation, including grasses with rhizomes and extensive fibrous root systems, herbs with above-ground runners and thicket-forming shrubs. If the soil binding capability of this vegetation is destroyed, a "blowout" occurs and if the vegetation is damaged extensively, the dunes begin shifting once again. Blowouts may reflect environmental conditions resulting from unusually high or low lake levels which cause changes within the beach area and weaken or destroy dune vegetation (Olson, 1958). In northern Michigan, westerly winds have blown out semicircular troughs with large horseshoe fronts illustrating the effects of predominant wind direction on dune formation (Waterman, 1917). On young dunes and foredunes, if sand covers the vegetation, the dunes begin to move burying more and more vegetation, starting a chain reaction of shifting dunes. Thus, only the "permanent" dunes farthest from the lake and well covered with vegetation escape the constant shifting, dune building and destroying processes.

Dune building is most extensive at the southern tip of Lake Michigan in Indiana and eastward and northward along the Michigan shore, due largely to the prevailing westerly winds.

In most instances, succession begins with xeric dune plants which in turn give way to pioneer shrubs and trees. The organic content of the sand increases gradually and in time moisture and nutrients may be adequate for invasion of the terminal mesic forest either of maple and beech or of maple, hemlock, yellow birch and other northern hardwoods. On the dunes, succession may be delayed or reversed by many factors. However, the general pattern is similar to that detailed below (Fig. 8).
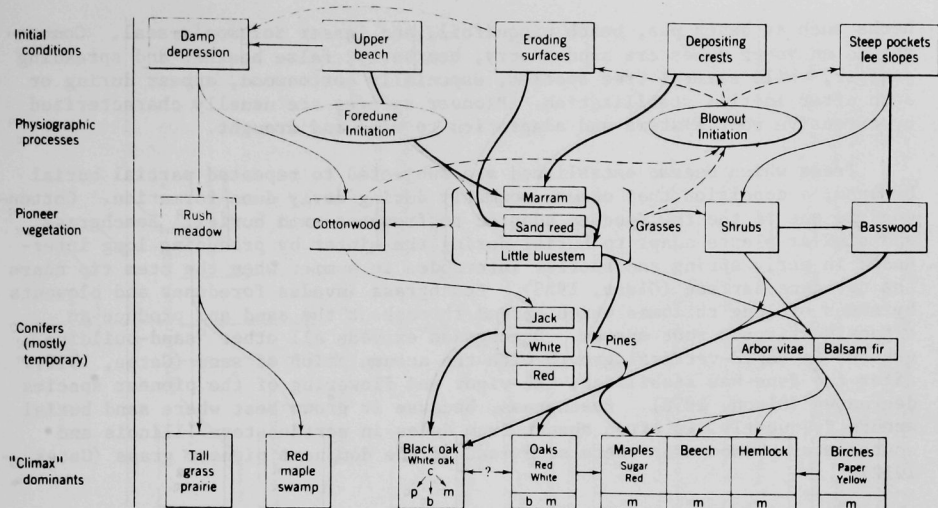
Fig. 8. Vegetational Succession on Diverse Dune Sites at the South End
of Lake Michigan. The usual successional pattern is shown in
the center with progression from dune grasses to pine and
finally oak forest. Low cover types, which vary with topog-
raphy, fire history, past vegetation, and water table include:
blueberry-huckleberry (b), choke cherry-poison ivy (c),
mesophytic herbs (m), and mixed grasses or "prairie" (p).
Successions in wet depressions (shown on the left) may termi-
nate in mesic prairie or hardwood swamp while those in pockets
in the dunes and on lee slopes (right) may develop into more
mesophytic forests of basswood, red oak and other species.
Moist areas in the southern Michigan dunes may support beech
and hemlock. From Olson (1958). (With permission, see credits.)

Primary dune succession begins with hardy, specially adapted, pioneer
species invading a xerophytic environment characterized by extremely high
daytime surface temperatures and by strong winds, both of which increase
transpiration and evaporation. In contrast, night temperatures may be very
low. Dry sand carried by strong winds sandblasts the vegetation, making
growth and seedling establishment difficult. These austere conditions are
further aggravated by relative sterility, low water holding capacity, and
susceptibility to nutrient leaching of the dune sands. The sand is often
moist to within a few centimeters of the surface. The surface layer of dry
sand serves as an effective insulator, preventing complete desiccation of the
dune sand making the growth of vegetation possible (Gates, 1912). However,
during the normal lifetime of most trees, extreme desiccation of the dunes
with a consequent die-back of vegetation may occur several times (Olson, 1958).

The initial invaders on a fresh dune may include beach grass (also called
dune grass or marram grass), sand reed, little bluestem and other grasses and

herbs such as beach pea, beach cinquifoil, and lesser Solomon's-seal. Common shrubs on young dunes are sand cherry, bearberry, false heather and spreading juniper, while several tree species, especially cottonwood, appear during or soon after initial stabilization. Pioneer species are usually characterized by extensive root systems and adaptation to wind and drought.

Trees which become established are subjected to repeated partial burial by sand, a condition that occurs commonly during early dune formation. Cotton-wood is one of the few species adapted to frequent sand burial. Beachgrass and similar plants adapt to burial during the winter by producing long inter-nodes in early spring and shorter internodes in summer when the stem tip nears the new dune surface (Olson, 1958). Beachgrass invades foredunes and blowouts by means of long rhizomes which spread throughout the sand and produce an extensive fibrous root system. Beachgrass exceeds all other "sand-building" grasses in rapid vertical growth with the accumulation of sand (Gates, 1912). After the dune has stabilized, the vigor and flowering of the pioneer species decreases (Olson, 1958). Beachgrass, because it grows best where sand burial occurs frequently, is often absent from dunes in northeastern Illinois and southeastern Wisconsin; there sand reed is the dominant pioneer grass (Gates, 1912).

Replacement of the pioneer community by forest is dependent upon soil moisture, nutrient availability, organic matter content and other factors, which result in numerous successional pathways toward a mesic condition (Fig. 9). Often a forest of jack pine with white pine and white birch becomes established, which may be replaced in time by black oak (southern xeric) forest.

In the smaller dunes of the dry northern Illinois and southern Wisconsin area, shrub communities gave way to black oak or southern xeric forest with wet prairie in the interdunal swales. Along the southeastern shore of Lake Michigan the moister climate resulted in the development of mesic forest of sugar maple, beech, basswood and red oak on the old stabilized dunes, particu-larly on lee slopes and in pockets. A similar situation was found in the dune areas of Door County, Wisconsin (Curtis, 1959), and along the northeastern and northern shores of the lake. There stands of red and white pine took the place of the black oak, northern mesic forest of maple, beech, hemlock and yellow birch was the terminal stage, and balsam fir and white cedar were found along the dune bases (Cowles, 1899; Waterman, 1917).

Southern xeric (black oak) forest has developed on many stabilized Lake Michigan dunes and is the terminal community on the oldest ones, the 12,000-year-old dunes in Indiana (Olson, 1958). Blueberry and huckleberry often invade the black oak forest as the soils become more acid. In some areas, mesic forest communities do not develop on even the oldest dunes. Soil con-ditions, rather than improving, may become less favorable with time; calcium and magnesium carbonates are leached out, soil moisture may remain low, seed may not be available and occasional fires favor black oak (Olson, 1958). Where steep lee slopes and damp depressions are present they may be invaded by basswood, which in turn may be followed by beech-maple mesic forest. Whichever successional route is followed and whatever forest community is terminal, about 1000 years appear necessary to reach terminal forest conditions on Lake Michigan dunes (Olson, 1958).

Fig. 9. Successional Patterns in the Vegetation of Beach and Dune Areas of Northeastern Illinois and Southeastern Wisconsin. The more important communities are indicated by capital letters. The beach and dunes succession along Lake Michigan terminated in a southern xeric black oak or oak-hickory forest association which eventually might progress to sugar maple. The aquatic and wet marsh communities associations (on the left of the diagram) presumably terminated in wet prairie. From Gates (1912).

The wet interdunal areas follow different successional patterns. At the south end of the lake wet swales were once common. As organic matter accumulated in the swales lowland forest communities developed; in contrast, wet prairie was common along the southwestern shore while in cooler and moister areas sedge meadow or northern lowland forest developed between the dunes. The wet swales in Indiana, Illinois, and southeastern Wisconsin are now absent or much reduced in area.

The relic dune area, lying on the sand plains near Seney, Michigan, in the Upper Peninsula, demonstrates another pattern of swale development. There in the wet areas between the dunes, a sphagnum and sedge mat became established and as the peat thickened acid sedge meadow developed. This community was soon invaded by low woody plants such as bog birch and leatherleaf. Water seepage across the tilted sand plain resulted in strips of these low shrubs forming fine striations at right angles to water flow producing a string bog. Although common farther north, string bogs are rare in the Basin, being evident elsewhere only in the Cedarburg Bog in Ozaukee County, Wisconsin. Today the dunes protrude above the Seney marsh as islands covered with pine, white birch and aspen forest (Heinselman, 1965).

OPEN WATER TO BOG SUCCESSION

As the glacial ice retreated from the Lake Michigan Basin it left behind great expanses of outwash sands pitted with depressions which retained water. Other lakes and wetlands formed in the low areas in ground moraines and in the kettles of recessional and interlobate moraines. Fine materials washed from the glacial debris accumulated in the depressions providing nutrients and helping to seal the basins from leakage. Many of these basins now support marsh, alder swamp, bog or swamp forest with extensive areas in the northern part of the Basin covered with sphagnum bog and conifer swamp communities.

Colonization began soon after the flow of meltwater ceased. An aquatic flora developed in the lakes and sedges and heaths colonized the beaches. Stands of emergent aquatic plants such as sedges, reeds and bur reeds developed in shallow bays and low places and peat began to accumulate.

In shallow water, plant growth and organic accumulation was rapid, sphagnum moss was abundant and the acid peat provided a substrate for conifer forest or for a dense shrub-carr which in turn was succeeded by lowland forest. The deeper depressions, small lakes and protected bays more often developed floating sphagnum-heath mats; in the northern part of the Basin, this successional process is evident today. Cores of peat from deposits in northern bogs suggest that successional development was often interrupted by natural calamities, flooding, drought or fire. The more mature communities have progressed through three stages; peat buildup, community stabilization and finally, degeneration.

Sphagnum bog communities in the Lake States have many similarities with those elsewhere in the northern hemisphere; presumably, this homogeneity derives from the fact that the sphagnum bog is " ... *very long-lived and, in terms of actual stability, far less liable to fluctuation than most of the stages that precede or follow it.*" (Curtis, 1959).

Sphagnum peat deposition may continue over very long periods; in some bogs of the Basin, peat has been accumulating, with occasional interruptions, since shortly after the retreat of glacial ice eight or ten thousand years ago.

One of the best known and readily observed successional sequences is that from open water to northern lowland, i.e., conifer swamp, forest. This sequence begins with the establishment of submerged aquatic plants and of a floating bog mat and it continues until the open water has been covered by the mat, the depression filled with peat and finally forest cover established on the sphagnum (Fig. 10). The details of this sequence are described below.
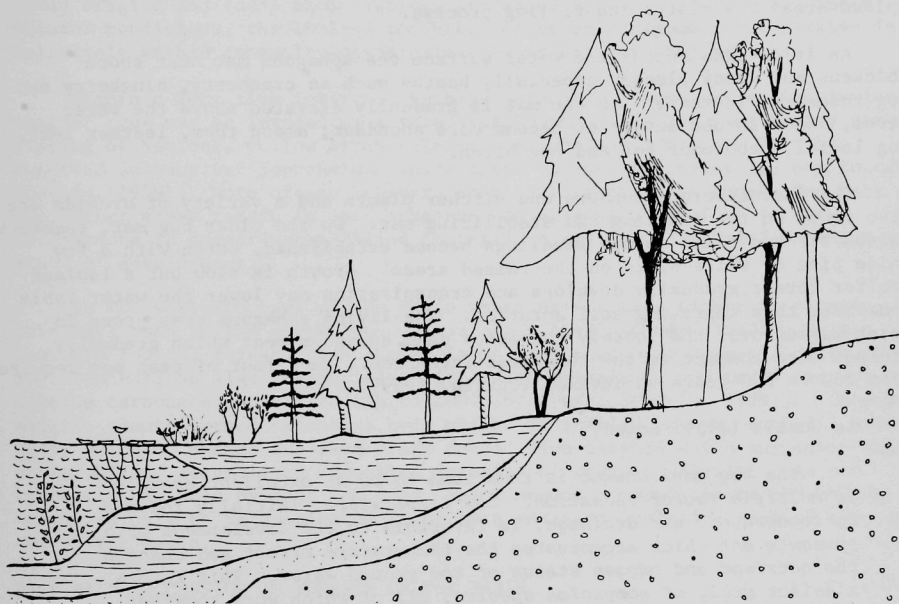
Fig. 10. Schematic Representation of Primary Succession from Lake through Bog toward Forest Vegetation.

Submerged aquatic plants such as pond weeds, eel grass, coontail, myriophyllum and stonewort become established in the deeper water. Shallower water supports floating species; among them are water lilies, water shield, bladderwort and emergent plants which include pickerel weed, arrowhead, spike rushes, reeds, bulrushes and sedges. These floating and emergent plants produce a massive network of roots and rhizomes as well as top material. At the same time a fringing mat of herbaceous and woody plants and sphagnum moss

begins to develop along the shore. The partially attached and partially floating mass gradually extends out over the water while beneath it a layer of peat begins to form. Bog mat plants include bog bean, sedges [*Carex lasicarpa*-- common in Wisconsin (Curtis, 1959) and *C. filiformis* in Michigan (Burns, 1904)], and other plants such as cranberry, cottongrass, leatherleaf, bog rosemary and sphagnum moss.

The shoreline fringe mat is susceptible to water level changes and to wave action. On large lakes, floating mats formed only in sheltered coves, small bays and inlets. High water may cause the breakup of extensive bog mats with the formation of floating bog islands. Mat formation is a relatively slow process and encroachment on the water surface may progress at only a few inches each century (Buell *et al.*, 1968). Material washed in from adjacent upland areas may hasten the filling process.

As it extends across the water surface the sphagnum mat near shore thickens and woody plants, especially heaths such as cranberry, blueberry and bog rosemary, increase. As the mat is gradually elevated above the water level, other shrubs invade or become more abundant; among them, leather leaf, bog laurel, laborador tea and bog birch.

The insectivorous sundews and pitcher plants and a variety of orchids are also found on the floating and stabilizing mat. On the older bog mat, tamarack, balsam fir and black spruce seedlings become established, often with a few white pine or white birch on the raised areas. Growth is slow but a lowland conifer forest gradually develops and transpiration may lower the water table somewhat, thus improving soil aeration. The living sphagnum moss grows in thick masses over the loosely compacted dead sphagnum peat which gradually becomes more compact as the thickness increases. Each foot of peat may require from 100 to 800 years to develop (Curtis, 1959).

As Curtis (1959) noted,

> *The bog environment is thus seen to be an excellent example of multiple factor causation. Low temperature, initially induced by topographic air drainage, is favorable to the development of a sphagnum mat which accentuates the temperature effect and changes the nutrient and oxygen status of the ground water. This favors a select group of companion species, all of which work together to maintain the conditions and prevent encroachment of other plants through antibiotic activity.*

Bog degeneration usually begins with some catastrophic event such as a major drought, fire or windthrow. Insect attacks may eliminate trees as the larch sawfly has done in the past. Windthrow is a common fate of the shallow rooted conifers that are growing on the poorly compacted sphagnum peat. When drought lowers the water table, the surface of the mat becomes dry and highly combustible. Fires may burn deep into the dry peat as they did during the drought years of the 1930's and thus eliminate the tree and shrub cover. Layers of sand, marl and charcoal interbedded with sphagnum and sedge peat suggest intervals of severe disturbance during postglacial time.

When the water level rises again, marsh or bog species reinvade the area and peat deposition resumes. If the major part of the sphagnum mat is destroyed a sedge meadow or an open marsh community may develop as the first step in reinitiating succession toward lowland forest. The nature of the new community will depend upon the nutrients available, the acidity of the soil and other factors.

The successional pattern described above occurred throughout the Lake Michigan Basin in postglacial time and a few relict tamarack swamps remained in northern Indiana until early in the present century. Northern lowland forests (tamarack or white cedar swamps) with a sphagnum mat occur within the Basin in Wisconsin and Michigan; the Cedarburg Bog in Ozaukee County, Wisconsin, is an example which has survived disturbance of both natural and human origins and today shows various stages of wetland succession. Under natural conditions, the lowland northern forest or sphagnum-conifer swamp is a relatively stable community which maintains itself for long periods.

Within a long time interval, perhaps several thousand years, the lowland conifer type may be invaded by a more mesic northern hardwood community consisting of hemlock, yellow birch, elm and perhaps sugar maple. This has occurred in many wet depressions where these wet-mesic forests are now found (Curtis, 1959). More often, however, some catastrophe sets succession back and many other areas remain in open sphagnum bog or lowland conifer forest. Successions in deeper water-filled depressions are today in the floating-mat stage of development.

In the southern part of the Basin where waters were richer in plant nutrients than in the north, succession often took pathways leading toward southern lowland forest. The deeper lakes supported heavy growths of stone-wort (*Chara*), an alga responsible, with other organisms, for large amounts of calcium carbonate deposition [up to 1000 lb/acre/yr (Curtis, 1959)]. Submerged aquatic plants formed extensive beds while, in shallow waters, cattail, arrow-head, bulrush, sedges and reed grass formed rich marshes which supported many waterfowl and accumulated extensive deposits of organic material. As the water was replaced by peat and muck, sedge meadow communities or shrub-carr developed only to be supplanted later by a southern lowland forest of elm, ash and silver maple.

POST-FIRE SUCCESSION IN FORESTS OF THE BASIN

Fire, set purposefully or accidentally by lightning, Indians, settlers, recreationists, loggers or locomotives, has always been a major agent in alteration of plant communities in the Lake Michigan Basin. The spring period between snow melt and "green-up" and the autumn period after leaf fall and before the first snow are the usual fire seasons in both grassland and forest. Historically, precipitation has varied greatly in timing as well as in amount, and the most severe fires have occurred in years of late summer and autumn drought.

There is ample evidence that the extensive white and red pine forests of Michigan and Wisconsin developed following fires in presettlement time (Graham, 1941; Stearns, 1950). The jack pine barrens were maintained by fires and remain high fire risk areas today. Some examples of fire related vegetation development are described in the following.

Jack Pine Fire Stands

The fires that ran through the pine-oak savanna killing some trees and burning the surface litter could also stimulate jack pine cones to open allowing seed to escape. When followed by conditions suitable for seedling survival, thickets of jack pine seedlings resulted, on occasion so dense that they were difficult to push through. Fires could "crown" readily in these low, dense thickets, devastating the stand and beginning the sequence again. Hill's oak responds to fire by sprouting from the base. Sprouts and good acorn production combine to maintain oak in the stands. Effective fire control in recent years has permitted jack pine stands to mature, forming extensive forests which are highly flammable. These stands are also susceptible to bud worm attack which may decimate large areas.

Red pine was associated with jack pine on slightly moister sites. If the young red pines survived fire for perhaps 50 years they developed a thick bark and a high crown providing immunity to normal ground fires. Patches of red pine are often found on the sandy "jack pine plains"; these trees usually show basal fire scars.

Aspen-Birch and Red Pine-White Pine Fire Successions

The post-fire successions involving red and white pine, aspen, white birch and associated species are more complex than those with jack pine. These successions function on a longer time cycle adjusted to the growth rates, seed production, sprouting ability and longevity of the tree species and to less frequent fires.

The fire sequence often began in red and white pine stands having an intermixture of older aspen, birch and perhaps red maple or northern red oak. The stage for a fire was set by a severe summer drought, windthrow or, during the last 100 years, by logging. The conflagration often began as a slow burning ground fire, consuming the dry litter, killing some saplings and burning in the debris at the bases of larger trees, thus producing the fire scars so typical of older pines. Wind might carry the ground fire into the tree crowns, perhaps flaring upward through a dead balsam fir, pile of slash or windthrown top. Burning hot with a following wind, the fire would move rapidly across large stands of pine leaving behind blackened trunks and dead crowns. On some occasions, the ground surface burned clean, on others litter and debris remained unburned. In all but the largest of wildfires, clumps of living trees would be left unburned in protected spots and often large or isolated veterans survived. These trees served as seed sources for the next stand.

White birch, aspen, and pin cherry develop open stands with an understory of shrubs such as blackberry, blueberry, hazel, a ground layer of bracken fern and various herbs. Pine seedlings may enter the stand immediately after the fire but are soon overtopped by faster growing aspen and birch.

Aspens (trembling and large-toothed aspen) are relatively short-lived species. After the first 20 or 30 years, stems begin to die and aspen species decrease in importance, gradually giving way to the longer-lived white birch. Pin and choke cherry are not tolerant of shade so they weaken and die after being overtopped by aspen or birch. Pines, if present in the stand, develop

gradually and after the initial stems mature seedlings may become established. In 50 or 60 years after the fire new seedlings indicate that progress toward a pine community is well under way.

Ground fires running through the older stand would eliminate balsam fir and kill some birch and red maple or oak stems but would only scar the older pines. The history of most pine stands in the Lake States is that of post-fire succession repeated in various combinations (Heinselman, 1973; Heinselman and Wright, 1973). On the sandy loam soils, pine forests reached great age and developed a heavy understory of maple and other broadleafed species.

There are many nuances to the pattern outlined above. The vagaries of weather, the impact of man, seed availability and substrate conditions all influence the results. However, it is evident that the general process of stand development, catastrophe, and regrowth has recurred many times since glacial time (Loucks, 1970).

NORTHERN HARDWOOD AND BEECH-MAPLE FOREST

The mesic terminal forests have often been assumed to be fireproof. However, although fire is relatively infrequent, it may occur and alter the course of stand development. In the deciduous forest, fires generally occur as ground fires during the spring or fall. Under these conditions small trees may be killed and larger ones scarred. Only during extreme drought or when abundant conifer slash was present did the fires become hot and destroy the overstory. Fire in hardwood stands may favor species whose seedlings develop best on bare soil, such as hemlock or yellow birch; high densities of those species can often be attributed to fire. Fire also eliminates the highly combustible understory species, balsam fir, and prevents the conversion of aspen, birch, and maple stands to fir. Fire in the mesic forest also encourages the entry of aspen and birch and for a period increases the diversity of the forest. In the beech-maple forest, fire aids in maintaining or increasing the proportion of less-shade tolerant oaks and hickories.

In most communities, frequent repeated fires result in deterioration of the remaining forest in which the trees, whether hardwood, pine or aspen, are stunted and poorly formed; white birch, red maple and red oak will be represented chiefly by stump sprouts.

FOREST DEVELOPMENT FOLLOWING LOGGING

Logging usually represents a less drastic perturbation than does fire. The soil surface, although scarified, is not completely destroyed and most of the organic matter remains on the ground. Seedlings and saplings already present are relatively undisturbed. However, the complete or partial removal of the overstory causes changes in the microclimate of the stand and may drastically alter the forest community.

Aspen stands, when logged, behave variously depending upon the degree of cutting. If the entire overstory is removed, the stand will respond with vigorous sprout growth which will soon progress toward a well-stocked aspen forest. If white birch, red maple, oak, or pine make up an appreciable portion of the stand, and if they are left uncut following an aspen sale, the shade

inhibits aspen sprout development and the ensuing stand may contain little or no aspen. Birch and red maple, if cut, will sprout and with clear cutting the new stand may resemble closely the one which preceded it.

Clear cutting in small areas of a few acres often produces frost pockets, especially in the northern hardwood forests. In these cases, aspen and cherry may invade, white ash abundance increases and sugar maple tends to diminish; a grass sod often develops (Levy, 1970). In contrast, under a regime of light and selective cutting, sugar maple is favored, as is beech in the beech-maple forests; both species grow well in relatively dense shade. Thus, the type or mode of cutting, as well as the prevailing conditions have much to do with future forest development.

Logging in oak stands can also produce directional effects on succession. In older oak stands where a maple, ash, beech, or similar secondary layer is beginning to develop, removal of the oak moves the stand more rapidly toward the terminal hardwood forest.

A shelterwood system, under which the stand is gradually opened up to permit the development of seedlings, is probably most effective for regenerating oak, although clearcutting may also produce a good second stand, largely of stump sprouts (Arend and Scholz, 1969).

Logging of conifer stands (red or white pine and hemlock-hardwood mixtures) may also shift the stand more rapidly toward the terminal maple forest. This is most likely to occur on loamy soils where a vigorous understory of maple or other hardwoods have become established under the larger pine or where these species are already mixed with hemlock. The shade cast by the deciduous forest and the rapid accumulation of leaf litter inhibit pine seedling growth and, without scarification or burning, natural regeneration of pine will not occur.

Similar developments can be described for other vegetation types, such as conifer swamps or spruce-fir forest.

As indicated in the preceding discussion, management practices may alter the direction or impede the progress of succession. Some of the management practices are directed towards arresting succession. This is evident whether the practice is clear cutting, selective logging or something as simple as mowing a lawn or pasture. It should be understood that all vegetation successions are not natural and that management methods have varying degrees of influence on vegetation development.

ANIMAL INFLUENCES ON SUCCESSION

No discussion of vegetation dynamics in the Basin would be complete without mention of the white-tailed deer (Dahlberg and Guettinger, 1956). The drastic disturbances caused by logging and associated fires, most evident in the period from about 1870 until 1920, resulted in huge areas of open land and brush; greatly increasing the acreage of deer range. Increased habitat, particularly summer range, combined with greater restrictions on hunting and elimination of the timber wolf, made possible a great increase in the size of the herd. Throughout the northern portion of the Lake Michigan Basin, winter

browsing by deer on woody plants became a major factor influencing forest regeneration. Certain species are preferred as food by the white-tail and in many northern areas hemlock, white cedar, and yellow birch seedlings have been reduced in number or totally eliminated. The regrowth of a few other species has, at least temporarily, been slowed. Deer may drastically influence composition of Basin forests, especially in the northern mesic and wet mesic regions. In the southern part of the Basin, where deer are not confined during the winter months, browsing has had little effect save on the highly preferred coniferous species.

In the southern portion of the region, pasturing of cattle has had similar effects in reducing seedling and sprout regeneration of woody plant species. Cattle trampling also causes soil compaction which, in turn, often results in the slow death of the overstory trees and a shift in species composition.

SUCCESSIONAL TRENDS ON ABANDONED FARMLAND

As they cleared the land for agricultural use, early settlers destroyed natural forest, savanna and prairie, interrupted natural succession on large acreages of the Lake Michigan Drainage Basin and greatly altered environmental conditions. Additional clearing and recent technological advances resulted in more and more land used for agriculture. Various considerations caused the abandoning of some of the farmlands creating what is known as the old fields. These old fields were left to natural vegetation development and succession.

Abandoned farmlands have a far different environment than that found in the native plant communities. Succession will not proceed in the same manner or at the same rate toward the natural climax community, as it would have prior to cultivation; the rate will instead depend on how greatly the soil conditions have been altered by cultivation and what propagules are available. In addition, community development will be influenced by past use of herbicides, insecticides and fertilizers and their effects on establishment and growth of various species. For example, in sandy fields large quantities of organic matter (manure) present at abandonment time may permit ragweed to become dominant in the first year rather than in the second or third (Thomson, 1943). Many weed species are ever-present in crop fields and remain as the pioneer species when the land is abandoned. Thomson (1943) speculated that successional development, which would result in white pine forests such as those originally covering large areas of the Wisconsin sand plains, was not likely to occur. Instead, centuries might be needed to replace the original organic matter lost from the soil by cultivation and fire.

Seed availability is especially important in old field succession. When the land is completely cleared, seedling establishment becomes largely a matter of chance. The proximity of a woodlot containing native species enhances the possibility that succession will eventually produce a regrowth of the original vegetation.

In the Lake Michigan Basin much abandoned farmland is held for land speculation and succession from field to forest is cut short by paving, building and the introduction of lawn grasses, ornamental shrubs and trees. Another large increment of cropland has been converted to pasture. Other areas set aside as preserves and game refuges may proceed through the entire successional

sequence. In addition to soil, climate, seed source, chance and historical considerations, the rate and course of succession is also dependent upon damage to vegetation and environmental disturbance associated with grazing and browsing.

If an old field is heavily grazed by cattle or browsed by deer, succession may be slowed or may retrogress depending on the duration and intensity of animal activity; pioneer species may reinvade as the woody species are eliminated or weakened (Evans and Cain, 1952; Evans and Dahl, 1955; Thomson, 1943).

On abandoned fields vegetation succession normally begins with annual weeds, followed by perennial weeds and grasses which, throughout the humid eastern United States, are usually replaced by shrubs and trees (Beckwith, 1954; Thomson, 1943; Odum, 1971).

The casual observer notes the changes: a blanket of annual grasses and weedy forbs soon covers the bare soil; within a year or two the annual plants are replaced by perennial grasses and forbs which form clumps and sod; soon shrubs and tree seedlings become visible; within a few years the field may support many shrubs and saplings which form a brushy cover; in time, the forest canopy closes in and the old field species disappear; finally, as the forest modifies its environment, the shade tolerant species increase, resulting in the development of the terminal community.

McCormick (1968) pointed out that changes in appearance do not necessarily imply complete shifts in composition of the vegetation. Shrub and tree species often become established with the annual weeds in the first year after abandonment. Elm, box elder and hawthorn and even more shade-tolerant or heavier seeded species may enter the field at the same time as dogwood or sumach but these trees do not become apparent for several years. The perennial forbs such as goldenrods and asters may persist until the pioneer woody plants are finally suppressed by a developing forest canopy.

Beckwith (1954) noted that "... *Early stages, including the rate of their succession, are influenced largely by the character of the last crop.*" In cultivated crops and small grain fields annual and biennial weedy plants were present even before abandonment, while perennial species occurred in the hay fields and pastures. Thus, the hay lands omit the annual weed stage but the established sod slows the rate of woody plant invasion behind that of the previously cultivated areas. The nature and rate of community development in the later stages of succession depends primarily upon climate, soil factors and disturbance, especially fire.

Depending upon soil fertility, moisture and climate, the annual weed stage may include such plants as pigweed, ragweed, lambs quarters (goosefoot), knotweed, wild mustard, crabgrass, foxtail grass, love grass, barnyard grass, witchgrass, purslane and bindweed. These plants soon disappear as the perennial grasses, for example Canada and Kentucky bluegrass, quackgrass, and timothy form sod; and as clumps of various goldenrods, asters, Canadian thistle, St. John's wort, wild strawberry and various clovers develop; and biennials such as whitetop and wild carrot appear.

Shrubby invaders may include red osier dogwood, smooth and staghorn sumach, willow species, blackberry, chokecherry and virginia creeper. Early tree invaders include American elm, black cherry, white ash, hawthorn, box elder, cottonwood and aspen. The species present again depend upon avail-ability of seed and conditions for establishment. The same factors apply to the gradual invasion of tolerant tree species and woodland forbs. Wet fields or particularly dry ones will show a different grouping of species adapted to conditions; usually succession will proceed more slowly under either wet or dry extremes.

The rate of succession on abandoned fields is generally rapid at first. The annual weeds may persist for one or two years, the perennial weed stage from 10 to 20 years or longer, depending upon the rate of shrub and tree invasion. Replacement of perennial forbs and grasses occurs gradually but after 20 to 40 years the initial woody canopy may be well developed (Fig. 11). Under unfavorable climatic or soil conditions, the perennial grass and forb stage may last for at least 80 years as observed in the northern part of the Basin (Levy, 1970).

In many areas of the Basin, especially in southern Michigan and eastern Wisconsin where environmental conditions and soils are favorable, maple-beech forest will become the terminal community. On the less fertile or dryer soils the succession may proceed to oak and hickory forest frequently with a major influx of black cherry as a result of grazing or drought (Auclair and Cottam, 1971).

Current emphasis on fire prevention makes succession to prairie or savanna unlikely. In central Wisconsin, where prairie remnants are common, abandoned fields are dominated by prairie species for the period from 15 to 22

|←————— VERTICAL SCALE ENLARGED —————→|←————— VERTICAL SCALE REDUCED —————→|
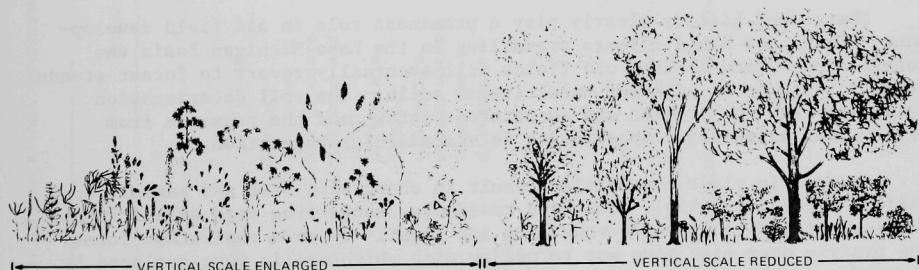
Fig. 11. Old Field Succession--an Idealized View. After abandonment, cultivated fields in the Lake Michigan Basin pass through several phases as they revert gradually to forest. The initial population of annual weeds is invaded by perennial grasses and forbs and by shrub and tree seedlings; gradually the field becomes a thicket of shrubs and as the trees grow larger the ground vegetation is shaded out and forest herbs may become established.

years after abandonment. Without fire, the prairie sod soon becomes frag-
mented into scattered patches while woody shrubby species invade and become
dominant (Table 5). By the 35th year, the jack pine-oak forest has become
well established, a major step to the establishment of the climax community
(Thomson, 1943).

An old field in Michigan (Evans and Cain, 1952) evidenced extremely slow
succession towards the oak-hickory deciduous forest, which originally covered
the area and which still existed along the periphery of the field. The field
had been extensively cultivated before 1900 and later pastured until about
1930, when it was converted to a reserve and protected from all disturbance
except for deer browsing. In 1952, the field still remained in a weedy grass-
land stage with few shrubs. Apparently heavy deer browsing and lowered soil
fertility from previous farming and pasturing prevented further development
(Evans and Cain, 1952). If the rate of succession was equivalent to that
observed on better sites in the Basin, the Michigan old field would now be a
well developed forest.

In the Michigan old field community, oak and hickory were only sparsely
established as individuals along the periphery of the field (Evans and Dahl,
1955). Several distinct types of grass communities were present, each under-
going change, depending upon their location in upland areas or in depressions
(Fig. 1). Evans and Dahl (1955) concluded that these communities had attained
a considerable degree of equilibrium with their environment. Evans and Cain
(1952) suggested that, *"Within the framework of succession there appear to be
more rapid micro-successional changes, which repeat themselves over and over
in the form of a cycle, marked by pioneer, building, mature, and degenerating
stages, with the established grasses representing the mature stage."* On this
site, further succession toward the deciduous forest, earlier predicted (Evans
and Cain, 1952), later appeared unpredictable if not doubtful (Evans and Dahl,
1955).

Chance and history clearly play a prominent role in old field develop-
ment. Under the humid climate prevailing in the Lake Michigan Basin the
normal expectation is that old fields will eventually revert to forest stands
similar to those on adjacent uncultivated soils. The soil deterioration
resulting from cultivation and associated factors and the pressure from
herbivorous animals are impediments to successful revegetation.

Changes in plant communities result in changes in bird and mammal popu-
lations (Beckwith, 1954). The bird residents change from seed eaters in the
earliest stages to insectivorous ones and finally to more omniverous forms.
The prairie deer mice give way to meadow mice which are in turn replaced by
white-footed mice. The presence of larger mammals and of predatory birds will
shift with changes in food and cover conditions. Thus, in the old field as
elsewhere, plant succession affects the entire biotic community.

Table 5. Successional Development on Abandoned Fields[a] in Central Wisconsin Sand Plains

	Years since Abandonment						Projected Trend
	1-2	3	4-9	9-15	15-22	22-37	37
Dominant species	Ragweed	Fleabane	--	--	Prairie species (15 yr)	Jack pine (37 yr)	Jack pine-oak forest climax
Associated species and successional trends	-Sandbur -Fleabane -Various American and European weeds -Canada bluegrass and a few prairie species including little bluestem	-Ragweed decreases -New invaders, milkweed and other perennials -Sandbur disappears except where there is disturbance	-Slow increase in diversity and number of prairie species	-Prairie species become prominent -Jack pine invading -Shrubs including smooth sumac and sweet fern becoming prominent	-Jack pine becoming prominent -Jack oak (Hill's) invading	-Sharp decrease in total population of prairie species, but diversity remains high -Sweet fern and hazelnut important shrub species -Large-toothed aspen prominent -Jack oak (Hill's) becoming prominent	-Jack pine -Jack oak -Black oak -Bur oak and associated understory

Compiled with data obtained from: Thomson, J. W., Jr., 1943.

[a]*Data was compiled by Thomson from observations over a period of 3 years using 13 various aged fields.*

APPENDIX A. SOURCE MAPS

A reader seeking further details is referred to the following list of specialized maps on the vegetational history or status of the Basin.

STATE MAPS

The early vegetation of Wisconsin. Wisconsin Geological and Natural History Survey, 1965.

Presettlement forests in Michigan. By J. O. Veatch, Dept. of Resource Dev., Michigan State University, 1959.

Natural vegetation of Indiana circa 1816. In: A. A. Lindsey, W. B. Crankshaw and S. A. Quadir. *Soil relations and distribution map of the vegetation of presettlement Indiana.* Bot. Gaz. 126:155-163. 1965.

Distribution of forest and prairie in Illinois about 1820. After R. C. Anderson, 1970. In: *A directory of Illinois nature preserves.* Illinois Dept. of Conservation and Illinois Nature Preserves Comm., 1972.

A preliminary vegetation map of Illinois. A. G. Vestal, Illinois State Acad. Sci. Trans. 23:204-217. 1931.

REGIONAL AND COUNTY MAPS

The swamps of Wisconsin. In: L. Martin, *The physical geography of Wisconsin.* Wisconsin Natural History Survey Bull. 36, 2nd ed. 608 p. 1927.

Sketch map of the northern parts of Emmet and Cheboygan counties, Michigan, showing the approximate locations of the major areas of bogland. In: F. C. Gates, *The bogs of northern lower Michigan.* Ecol. Monogr. 12:213-254. 1942.

Map showing distribution of prairies in Michigan. In: J. O. Veatch, *Dry prairies of Michigan.* Papers Michigan Acad. Sci., Arts and Letters. 8:269-278. 1927.

The original areas of prairie in southeastern Wisconsin. In: L. Martin, *The physical geography of Wisconsin.* Wisconsin Natural History Survey Bull. 36, 2nd ed. 608 p. 1927.

Vegetation types of the northern third of Indiana in 1830, as determined from original land survey records and modern large scale soil maps of counties. In: A. A. Lindsey, *Vegetation of the drainage-aeration classes of northern Indiana soils in 1830.* Ecology 42:432-436. 1961.

Forest association map of southwestern Michigan. <u>In</u>: L. A. Kenoyer, *Forest distribution in southwestern Michigan as interpreted from the original land survey*. Michigan Acad. Sci., Arts and Letters, 19:107-111. 1933.

Plant associations in Barry, Calhoun and Branch counties. L. A. Kenoyer. *Plant associations in Barry, Calhoun and Branch counties, Michigan, as interpreted from the original land survey*. Michigan Acad. Sci., Arts and Letters, 25:75-77. 1940.

Map of Kalamazoo County, Michigan, indicating the original plant associations. L. A. Kenoyer. *Ecological notes on Kalamazoo County, Michigan, based on the original land survey*. Papers Michigan Acad. Sci., Arts and Letters 11:211-217. 1929.

Pioneer landscapes of Kalamazoo County, Michigan. B. C. Peters. *Pioneer evaluation of Kalamazoo County landscape*. The Michigan Acadamician, III:15-25. 1970.

Map of Missaukee County showing the primeval forest as interpreted from the original land survey field notes of 1854. <u>In</u>: J. C. Elliott. *The phytosociology of the upland second growth hardwoods of Missaukee County, Michigan*. Michigan State University, Ph.D. thesis. 1954.

Forest map of Ottawa County, Michigan. L. A. Kenoyer. *Forest associations of Ottawa County, Michigan, at the time of the original land survey*. Papers Michigan Acad. Sci., Arts and Letters 28:47-49. 1942.

APPENDIX B.   COUNTY DESCRIPTIONS

The following county descriptions are based on information from the Soil Survey Reports issued by the USDA Soil Conservation Service in cooperation with various state agencies. Specific counties were chosen from more recent reports to facilitate the interpretation of modern forest and agricultural maps.

WISCONSIN

Racine and Kenosha counties -- issued December 1970

In 1836, when the first white settlers were plowing the prairie and cutting trees for cabins, 60 to 65% of the area that is now Kenosha and Racine counties was covered with trees, chiefly oaks, growing in sparse or open stands. The remainder was mostly prairie. Today, woodland occupies less than 7% of the two counties. About two-thirds of the present woodland is oak, principally red and white oak. Other important tree species are hickory, red maple, sugar maple, basswood and cherry. Most of the forested areas are privately owned small woodlots; nearly half are heavily grazed. Acreage of Christmas tree plantations is expanding, and an even larger acreage is anticipated for this purpose.

Dairying is the chief source of income for farmers in these counties. Farming is diversified, however, and truck crops are important in the farm economy. Corn is the principal crop and alfalfa the leading forage crop.

Currently, 69% of the land area is cropland, 9% pasture, 7% woodland and 7% marsh and wildlife refuge. By 1975, if present trends continue, the acreage of cropland will decrease by 20%, permanent pasture by 52% and woodland by 21%. Acreages of marsh and wildlife land will increase by 8% and urban uses by 155%.

In the east, along Lake Michigan, these two counties have a 190-day growing season and in the west, one of 173 days. Annual precipitation is approximately 32 inches.

Ozaukee County -- issued September 1970

Forests originally covered 94% of Ozaukee County. The remainder was in marshes, and these were mainly in the area now comprising Cedarburg, Fredonia and Saukville townships.

The original forests consisted mainly of maple, beech, basswood, and hemlock. Some walnut and a few scattered pines were included. Early logging removed nearly all of the merchantable timber, and about 11% of the county is now wooded. The present woodland consists of lowland and upland hardwoods. These wooded areas add to the esthetic and recreational values of the county and provide shelter and food for wildlife.

In the swamps of the county, the tree vegetation was mainly black ash, elm, cedar and tamarack, i.e., northern and southern lowland forests. Sedge, cattail and grass marshes were common. Many bog forests and marshes remain in the county.

Wetland forests form the major wooded areas in trees, and the 2000 acre Cedarburg Bog in Saukville Township is the largest single wooded area. The bog soils and those in many lowland woods are predominantly organic with a high water table.

The wetlands have not been drained for cropland either because outlets for water are not available or because the cost of clearing and of draining the areas is greater than the value of the land for crops.

Upland woods average 3 to 10 acres and have not been developed for crops or pasture because they are too steep or the acreage is too small. Native trees in upland woods are hardwoods such as maple, ash, oak, basswood, hickory, elm, beech and ironwood. Some red and white pine have been planted.

The upland woodlots have greater value for recreation and esthetics or for future residential sites than they have for timber. Proximity to the Milwaukee metropolitan area has raised land values and encouraged speculative development. Many of the wooded areas adjoin cropland, and could be improved as wildlife areas by planting shrubs along their borders.

Farming, based on dairying, is the most important enterprise in Ozaukee County. Farmland accounts for 72% of the total acreage; of this, 66% is cropland and about 4% permanent pasture.

The climate and soils in Ozaukee County are favorable for grain crops and hay, which occupy the largest crop acreages. These crops are fed directly on the farms to dairy cattle or to other livestock. Alfalfa is first in acreage planted, followed closely by corn and oats. Half the corn crop is harvested for grain and half for silage.

The acreage in hay has remained fairly constant for the last ten years. Alfalfa and bromegrass make up about 90% of the tame hay grown. Clover, timothy and mixtures of clover and grasses form the balance.

The acreage in oats is gradually decreasing, but it remains the principal small grain crop. Wheat, barley, buckwheat, rye, and soybeans are grown in small amounts varying from year to year. Most small grains are fed to the livestock.

Vegetables are grown for cash crop (3522 acres in 1964). Of these, sweet corn, green peas, and snap beans were most important. Sweet corn and green peas are grown mainly for canning. Beets, tomatoes, cabbage, cucumbers and other vegetables also are grown for the market on some farms. The apple harvest in the county amounted to 3.5 million pounds (from 17,731 trees) in 1964.

Annual precipitation is generally adequate. The average growing season is 146 days, although near Lake Michigan it may extend to 162 days.

Washington County -- issued June 1971

Native vegetation was very similar to that of adjoining Ozaukee County although areas of oak forest were more common.

About 75% of the acreage of Washington County is cropland. Oats, alfalfa and corn are the main crops with corn occupying the largest acreage. Lesser crops are wheat, barley, rye, potatoes, peas, sweet corn and red beets. Red beet production is highest in the state. Farming, mainly dairying, is the major enterprise in Washington County. Approximately 15% of the farmland in the county is in permanent pasture, consisting mostly of native grasses.

Annual precipitation, averaging almost 30 inches, is normally adequate for the crops. Although the supply of moisture is low in July and August, a severe drought that damages all crops is rare. The length of the growing season varies greatly, 160 days in the eastern portion of the county to 130 days in the western part.

ILLINOIS

Lake County -- issued September 1970

When the first settlers came, much of Lake County was forested with excellent stands of oak, hickory, maple and other hardwoods. Tamarack covered many swampy areas of Houghton peat soils.

Today, the remaining woodland consists of understocked stands of poor quality trees. Only one area of significant size remains in tamarack and it belongs to the State of Illinois.

By far the largest farm acreage is in corn. Farmland is used predominantly for cash crops.

The annual precipitation is 33 inches and the growing season is 155 days.

INDIANA

Lake County -- issued July 1972

The native vegetation of this county consisted of deciduous hardwood forest, dry and wet prairie, marsh and lowland forest.

In 1880, about 74% of the county was used for farming. Urbanization reduced this acreage to 53.4% by 1964. Row crops, small grains and hay crops are the principal crops which include corn, soybeans and hay meadow.

The annual precipitation is about 36 inches. From the Lake Michigan area to the lowlands in the southern part of the county, the length of the growing season varies greatly. In the northern part of the county, the average date of the last frost in spring occurs during the last week of April, but in the lowlands it occurs on or about May 10. In fall, the average date of the first frost in the north is about October 16, but in the south it occurs about two weeks earlier. Thus, the growing season in southern Lake County is several weeks shorter than in the north.

MICHIGAN

Osceola County -- issued June 1969

Agriculture was slow to develop in Osceola County. The early settlers found the county clothed with a dense forest. The sandy soils were covered with red pine, jack pine and scattered clumps of hardwoods. The clayey soils supported hardwoods that included oak, hard maple, sugar maple, beech, elm, yellow birch, ash, cherry, basswood and some hemlock. In the swamps and bogs and on stream bottoms, the major trees were spruce, tamarack, white cedar, and balsam fir. Pines were logged first, then the hardwoods. Aspen and birch are dominant in the present forests.

Fifty percent of the county is in state forest, privately owned woods, abandoned farms, with some industrial and urban sites. The other fifty percent is farmland; dairy farming dominates. The 1964 Census of Agriculture lists alfalfa, hay, corn, mixtures of clover and grasses cut for hay, oats, and wheat as the principal crops grown in order of decreasing acreage. The chief cash crops are potatoes and wheat.

The average growing season is 125 days and the annual precipitation is 30 inches.

Muskegon County -- issued October 1968

Muskegon County originally was covered almost entirely by forest. White oak, beech and maple grew on the finer textured soils in morainic areas, and pine was common in the sandy parts of the county. High quality hard maple still grows in the county. The white pine cut for timber is being replaced, in small part, by plantations of pines grown for Christmas trees. Fifty percent of the land area of the county is still woodland, most privately owned. The public land is largely in the Manistee National Forest. Much of the woodland is on droughty, infertile soils where trees are black and white oaks of low quality; in places the understory is white pine.

Agriculture is the principal enterprise in Muskegon County and corn, wheat and timothy-clover are the major crops, in that order. Dairy cows and other livestock are kept on most farms.

Fruit crops are an important source of income. Orchards are prevalent and include, in order of importance, cherries, apples, peaches, pears and plums.

Because of the prevailing westerly winds, there is a strong lake influence. Winters are milder, summers are cooler, and snowfall is greater than areas more distant from the lake. Annual precipitation is 31 inches and the growing season near Grand Rapids is from May 4 to November 6 and at Muskegon from May 18 to October 19.

Ionia County -- issued December 1967

Forests originally covered most of Ionia County; clearing the land for farming and cutting timber for commercial purposes eventually eliminated the virgin stands. The woodland now consists mainly of second and third growth stands.

Eighty percent of the land is in farms, the rest consists mainly of state forest. Of the farmland, 54% is in harvested crops and 8% is pasture. Corn is the chief row crop, and small grains, in order of importance, are wheat, oats, barley, rye and buckwheat. Alfalfa and clover are important hay crops.

Many other crops make up the remaining 38% of farmland. Small areas of organic soils are used for mint, celery and other vegetables. Potatoes are commonly grown on the sandier soils, mostly in the northwestern part of the county. Many farmers grow white beans as a cash crop.

Alfalfa can be grown if the soils are adequately limed. Small grain has been grown traditionally, partly as a cover for alfalfa seedlings. If fertilized, hybrid corn can be grown successfully except on sandy soils. Hybrid corn has been a boon to the county because it matures earlier than the older open-pollinated corn.

Dairy farms are numerous. Other farms specialize in fruits, mainly apples. Strawberries, raspberries, pears and peaches are also grown. Ionia County is too far from Lake Michigan to benefit greatly from the moderating effect of the lake and peaches are grown with considerable risk of freezing.

The annual precipitation is about 33 inches; the average growing season is 135 days at the Saranac Weather Station and 157 days at the Webber Dam Station.

CREDITS

The authors and the Argonne National Laboratory gratefully acknowledge John Wiley and Sons, Inc., New York for permission to use Figure 12.6, p. 441, in *Elements of Ecology* by George L. Clarke, 1954, on which they hold the copyright, as our Figure 8.

REFERENCES CITED

Anderson, G. W. 1972. *Diseases*. <u>In</u>: *Aspen Symposium proceedings*. USDA Forest Service. Gen. Tech. Rep. NC-1. pp. 74-82.

Anderson, R. C. 1970. *Prairies in the Prairie State*. Trans. Illinois Acad. Sci. 63:214-221.

Arend, J. L., and H. F. Scholz. 1969. *Oak forests of the Lake States and their management*. USDA Forest Service. Research Paper NC-31. 36 p.

Auclair, A. N., and G. Cottam. 1971. *Dynamics of black cherry (Prunus serotina Erhr,) in southern Wisconsin oak forests*. Ecol. Monogr. 41:153-177.

Barnes, B. V. 1966. *The clonal growth habit of American aspens*. Ecology 47:439-447.

Bayley, C. C. 1954 *Western trip*. Wis. Mag. Hist. 37:237-239.

Beckwith, S. L. 1954. *Ecological succession on abandoned farm lands and its relation to wildlife management*. Ecol. Monogr. 24:348-376.

Benninghoff, W. S. 1964. *The prairie peninsula as filter barrier to post-glacial plant migration*. Proc. Indiana Acad. Sci. 73:116-124.

Bird, J. N. 1948. *Early and late types of red clover*. Sci. Agr. 28:444-453.

Blake, G. M. 1964. *Clone identification and delineation in the aspens*. Diss. Abstr. 25:2688.

Braun, E. L. 1950. *Deciduous forests of eastern North America*. The Blakiston Co., Philadelphia, 596 p.

Bray, J. R. 1956. *Gap phase replacement in a maple-basswood forest*. Ecology 37:598-600.

Brewer, R. 1965. *Vegetational features of a wet prairie in southwestern Michigan*. C. C. Adams Center for Ecological Studies. Occ. Papers, No. 13. 16 p.

Brown, R. T. 1950. *Forests of the Central Wisconsin sand plains*. Bull. Ecol. Soc. Amer. 31:56.

Buell, M. F., H. F. Buell, and W. A. Reiners. 1968. *Radial mat growth on Cedar Creek Bog, Minnesota*. Ecology 49:1198-1199.

Burns, G. P. 1904. *Formation of peat in Dead Lake* (Abstract). Papers, Michigan Acad. Sci. 6:76-77.

Bushnell, T. M. 1942. *Some aspects of the soil catena concept.* Proc. Soil Sci. Soc. Amer. 1:466-476.

Butler, J. E. 1954. *Interrelations of autecological characteristics of prairie herbs.* Ph.D. thesis. Univ. Wisconsin, Madison.

Cain and Slater. 1948. *The vegetation of Sodon Lake.* Am. Midland Naturalist 40:741-762.

Chase, C. D. and R. E. Pfeifer. 1969. *The growing timber resources of Michigan, 1966, Eastern Upper Peninsula.* Michigan Dept. Natural Resources, East Lansing. 66 p.

Chase, C. D., R. E. Pfeifer, and J. S. Spencer, Jr. 1970. *The growing timber resource of Michigan, 1966.* No. Cent. Forest Exp. Sta. USDA Forest Service Resource Bull. NC-9. 62 p.

Chase, C. D., and N. R. Thompson. 1967. *Potato production in Michigan.* Michigan State University Cooperative Extension Service. Extension Bull. 546. East Lansing. 14 p.

Cooper, Fennimore. 1848. *The oak openings.* New York.

Cooper, W. S. 1913. *The climax forest of Isle Royale, Lake Superior, and its development.* Bot. Gaz. 55:1-44, 115-140, 189-235.

Costello, D. F. 1936. *Tussock meadows in southeastern Wisconsin.* Bot. Gaz. 97:610-649.

Cottam, G. 1949. *The phytosociology of an oak woods in southwestern Wisconsin.* Ecology 30:271-287.

Cowles, H. C. 1899. *The ecological relations of the vegetation on the sand dunes of Lake Michigan.* Bot. Gaz. 27:95-117, 167-202, 281-308, 361-391.

_____. 1901. *The physiographic ecology of Chicago and vicinity.* Bot. Gaz. 31:73-108, 145-182 (also printed as Geog. Soc. Chicago Bull. No. 2:1-76, 1901).

Curtis, J. T. 1955. *A prairie continuum in Wisconsin.* Ecology 36:558-566.

_____. 1959. *The vegetation of Wisconsin.* Univ. of Wisconsin Press, Madison, Milwaukee, and London. 657 p.

_____, and G. Cottam. 1950. *Antibiotic and autotoxic effects in prairie sunflower.* Bull. Torrey Bot. Club 77:187-191.

_____, and H. Greene. 1949. *A study of relic Wisconsin prairies by the species-presence method.* Ecology 30:83-92.

_____, and R. P. McIntosh. 1951. *An upland forest continuum in the prairie-forest border region of Wisconsin*. Ecology 32:476-496.

Dahlberg, B. L., and R. C. Guettinger. 1956. *The white-tailed deer in Wisconsin*. Wisconsin Cons. Dept., Tech. Wildlife Bull. 14. 282 p.

Essex, B. L., and D. A. Gansner. 1965. *Illinois' timber resources*. Lake States Forest Exp. Sta. USDA Forest Service Resource Bull. LS-3. 56 p.

Evans, F. C., and S. A. Cain. 1952. *Preliminary studies on the vegetation of an old-field community in southeastern Michigan*. Univ. Michigan, Contr. Lab. Vert. Biol. 51:1-17.

_____, and E. Dahl. 1955. *The vegetational structure of an abandoned field in southeastern Michigan and its relation to environmental factors*. Ecology 36:685-706.

Farmer, R. E., Jr. 1962. *Aspen root sucker formation and apical dominance*. Forest Sci. 8:403-410.

Fralish, J. S. 1972. *Youth, maturity and old age*. In: *Aspen Symposium proceedings*. USDA Forest Service. Gen. Tech. Rep. NC-1. pp. 52-57.

Garland, H. 1972. *Trends and prospects for wood products*. In: *Aspen Symposium proceedings*. USDA Forest Service. Gen. Tech. Rep. NC-1. pp. 35-39.

Gates, F. C. 1912. *The vegetation of the beach area in northeastern Illinois and southeastern Wisconsin*. Bull. Ill. Lab. Nat. Hist. 9:255-372.

_____. 1942. *The bogs of northern lower Michigan*. Ecol. Monogr. 12:213-54.

Gleason, H. A. 1901. *The flora of the prairies*. B.S. thesis, Univ. Illinois.

_____. 1926. *The individualistic concept of the plant association*. Bull. Torrey Bot. Club 53:7-26.

Graham, S. 1941. *Climax forests of the Upper Peninsula of Michigan*. Ecology 22:355-372.

Graham, S. A., R. P. Hanison, Jr., and C. E. Westell, Jr. 1963. *Aspen-Phoenix trees of the Great Lakes Region*. Univ. of Michigan Press, Ann Arbor. 272 p.

Guire, K. E., and E. G. Voss. 1963. *Distributions of distinctive shoreline plants in the Great Lakes Region*. Mich. Bot. 2:99-114.

Hansen, H. L., and V. Kurmis. 1972. *Natural succession in north-central Minnesota*. In: *Aspen Symposium proceedings*. USDA Forest Service. Gen. Tech. Rep. NC-1. pp. 59-66.

Harrison, C. M., and J. F. Davis. 1966. *Reed canary grass for wet lowland areas of Michigan.* Michigan State University Cooperative Extension Service. Extension Bull. E-517. East Lansing. 4 p.

Heinselman, M. L. 1954. *The extent of natural conversion to other species in the Lake States aspen-birch type.* J. Forestry 52:737-738.

_____. 1965. *String bogs and other patterned organic terrain near Seney, upper Michigan.* Ecology 46:185-188.

_____. 1973. *Fire in the virgin forests of the Boundary Water Canoe Area, Minnesota.* J. Quart. Res. 3:329-382.

_____, and H. E. Wright. 1973. *The ecological role of fire in natural conifer forests of western and northern North America. A preface.* J. Quart. Res. 3:317-318.

Hough, A. F. 1943. *Soil factors and stand history in a virgin forest valley on the northern Allegheny Plateau.* Soil Science 56:19-29.

Hudgins, B. 1948. *Michigan geographic backgrounds in the development of the commonwealth.* Edwards Bros., Inc. Ann Arbor, Mich. 104 p.

Hull, J., Jr. 1970. *Commercial strawberry culture in Michigan.* Michigan State University Cooperative Extension Service. Extension Bull. E-682. East Lansing. 12 p.

_____, D. Ricks, D. Smith, G. McManus, J. Lincoln, F. Kackle, W. MacLean, H. Belter, and G. Antle. 1973. *The Michigan fruit industry. In: Fruit, vegetables, bees and pollination--now and in 1985.* Michigan State University Agricultural Experiment Station, Research Report 188. East Lansing. 28 p.

Johnston, S., and J. E. Moulton. 1968. *Blueberry distribution, variety evaluation and breeding in Michigan.* Michigan State University Agricultural Experiment Station, Research Report 67. East Lansing. 7 p.

_____, J. E. Moulton, and J. Hull, Jr. 1969. *Essentials of blueberry culture.* Michigan State University Cooperative Extension Service. Extension Bull. E-590. East Lansing. 16 p.

Keays, J. L. 1972. *The resource and its potential in North America. In: Aspen Symposium proceedings.* USDA Forest Service. Gen. Tech. Rep. NC-1. pp. 4-9.

Kendall, W. A. 1958. *The persistence of red clover and carbohydrate concentration in the roots at different temperatures.* Agron. J. 50:657-659.

Kenoyer, L. A. 1933. *Forest distribution in southwestern Michigan as interpreted from the original land survey (1826-32).* Papers, Michigan Acad. Sci. 19:107-111.

Klebesadel, L. J., and D. Smith. 1958. *The influence of oat stubble management on the establishment of alfalfa and red clover.* Agron. J. 50:680-683.

Kohnke, H., and L. S. Robertson. 1966. *Changing patterns of agriculture.* In: *Natural features of Indiana.* A. A. Lindsey, ed. Indiana Acad. Sci. pp. 519-531.

Leuschner, W. A. 1972. *Projections of inventories in the Lake States.* In: *Aspen Symposium proceedings.* USDA Forest Service. Gen. Tech. Rep. NC-1. pp. 10-15.

Levy, G. F. 1970. *The phytosociology of northern Wisconsin upland openings.* Am. Midland Naturalist 83(1):213-237.

Lindsey, A. A. 1961. *Vegetation of drainage-aeration classes of northern Indiana soils in 1830.* Ecology 42:432-436.

_____, (ed.) 1966. *Natural features of Indiana.* Indiana Acad. of Sci. Sesquicentennial Vol. Indianapolis, Indiana. 600 p.

Livingston, B. E. 1903. *The distribution of upland plant societies of Kent County, Michigan.* Bot. Gaz. 35:36-55.

Loucks, O. L. 1970. *Evolution of diversity, efficiency and community stability.* Amer. Zool. 10:17-25.

Maini, J. S., and K. W. Horton. 1966. *Vegetative propagation of Populus spp.* I. *Influence of temperature on formation and initial growth of aspen suckers.* Can. J. Bot. 44:1183-1189.

Martin, L. 1932. *The physical geography of Wisconsin.* Bull. Wis. Geol. and Nat. Hist. Surv. 36. Madison. 608 p.

Maycock, P. F., and J. T. Curtis. 1960. *The phytosociology of boreal conifer-hardwood forests of the Great Lakes Region.* Ecol. Monogr. 30:1-35.

McCormick, J. 1968. *Succession: prelude.* Grad. School of Fine Arts, Univ. Pennsylvania.

McGuire, J. R. 1972. *Some problems and issues in managing the aspen resource.* In: *Aspen Symposium proceedings.* USDA Forest Service. Gen. Tech. Rep. NC-1. pp. 1-3.

McIntosh, R. P. 1957. *The York Woods, a case history of forest succession in southern Wisconsin.* Ecology 38:29-37.

Michigan Department of Agriculture. 1972. *Michigan Agricultural Statistics.* Mich. Dept. of Agr., East Lansing, 47 p.

Odum, E. P. 1971. *Fundamentals of ecology.* 3rd Ed. W. B. Saunders Co., Philadelphia. 574 p.

Olson, J. S. 1958. *Rates of succession and soil changes on southern Lake Michigan sand dunes.* Bot. Gaz. 119:125-170.

Pepoon, H. S. 1927. *An annotated flora of the Chicago area.* Chicago Acad. Sci., Chicago. 554 p.

Perala, D. A. 1972. *Regeneration: biotic and silvicultural factors.* In: *Aspen Symposium proceedings.* USDA Forest Service. Gen. Tech. Rep. NC-1. pp. 97-102.

Peters, B. C. 1970. *Pioneer evaluation of the Kalamazoo County landscape.* Michigan Academician. III:15-25.

Petty, R. O., and M. T. Jackson. 1966. *Plant communities.* In: *Natural features of Indiana.* A. A. Lindsey, ed. Indiana Acad. Sci. pp. 264-296.

Pfeifer, R. E., and J. S. Spencer, Jr., 1969. *The growing timber resources of Michigan, 1966, northern Lower Peninsula.* Michigan Dept. of Natural Resources, East Lansing. 112 p.

Roth, F. 1898. *On the forestry conditions in northern Wisconsin.* Wisconsin Geol. and Nat. Hist. Surv. Bull. I. Econ. Series I. 78 p.

Sandberg, D., and A. E. Schneider. 1953. *The regeneration of aspen by suckering.* Univ. Minnesota, Minnesota Forestry Notes 24, 2 p.

Scharrer, E. M. 1971. *Current evidence of tall-grass prairie remnants in southwestern Michigan.* M.S. thesis. Michigan State Univ. 139 p.

Sherff, E. E. 1912. *The vegetation of Skokie Marsh, with species references to the subterranean organs and their interrelationships.* Bot. Gaz. 53:415-435.

_____. 1913. *Vegetation of Skokie Marsh.* Bull. Illinois Lab. Nat. Hist. 9:575-614.

Smith, D. 1957. *Flowering responses and winter survival in seedling stands of medium red clover.* Agron. J. 49:126-129.

_____. 1960. *Forage management in the north.* Kendall-Hunt Pub. House. Dubuque, Iowa. 219 p.

Spencer, J. S., Jr., 1969. *Indiana's timber (1967).* No. Cent. Forest Exp. Sta. USDA Forest Service Resource Bull. NC-7. 61 p.

_____, and R. E. Pfeifer. 1969. *The growing timber resources of Michigan, 1966, western Upper Peninsula.* Michigan Dept. of Natural Resources, East Lansing. 72 p.

_____, and H. W. Thorne. 1972. *Wisconsin's 1968 timber resource.* No. Cent. Forest Exp. Sta. USDA Forest Service Resource Bull. NC-15. 80 p.

Stearns, F. W. 1949. *Ninety years change in a northern hardwood forest in Wisconsin*. Ecology 30:350-358.

_____. 1950. *The composition of a remnant of white pine forest in the Lake States*. Ecology 31:290-292.

_____. 1965. *Present and future status of forests along surface waters of the North Central States*. In: Wood duck management and research. Wildlife Management Inst. pp. 5-22.

Telford, C. J. 1926. *Third report on a forest survey of Illinois*. Bull. Illinois Nat. Hist. Surv. 16. 102 p.

Tesar, M. B., and S. C. Hildebrand. 1966. *Reestablishment of pastures and hay fields in one year*. Michigan State University Cooperative Extension Service. Extension Bull. 527. East Lansing. 4 p.

Therrien, H. P., and D. Smith. 1960. *The association of flowering habit with winter survival in red and alsike clover during the seedling year of growth*. Can. J. Plant Sci. 40:335-344.

Thompson, P. W. 1972. *The preservation of prairie stands in Michigan*. Proc. 2nd Midwest Prairie Conf. 1970. Madison, Wis. pp. 13-14.

Thomson, J. W., Jr., 1943. *Plant succession on abandoned fields in the central Wisconsin sand plain area*. Bull. Torrey Bot. Club 70:34-41.

Transeau, E. N. 1905. *The bogs and bog flora of the Huron River Valley*. Bot. Gaz. 40:351-374, 418-448 (1905). 41:17-42 (1906).

_____. 1935. *The prairie peninsula*. Ecology 16:423-437.

Veatch, J. O. 1928. *The dry prairies of Michigan*. Papers, Michigan Acad. Sci. 8:269-278.

_____. 1932. *Soil maps as a basis for mapping original forest cover*. Papers, Michigan Acad. Sci. 15:267-273.

_____. 1959. *Presettlement forest in Michigan*. A map. Dept. of Resource Development, Michigan State University, East Lansing. 1931.

Vestal, A. G. 1931. *A preliminary vegetation map of Illinois*. Trans. Illinois Acad. Sci. 23:204-217.

Ware, G. H. 1955. *A phytosociological study of lowland hardwood forests in southern Wisconsin*. Ph.D. thesis. Univ. Wisconsin, Madison.

Waterman, W. G. 1917. *Ecology of northern Michigan dunes: Crystal Lake Bar Region*. Papers, Michigan Acad. Sci. 19:197-207.

White, K. L. 1965. *Shrub-carrs of southeastern Wisconsin*. Ecology 46:286-304.

Whitford, P. B. 1958. *A study of prairie remnants in southeastern Wisconsin.* Ecology 39:727-733.

_____, and K. Whitford. 1956. *Ellery Channing in Illinois. An ecological reconstruction of the land bought by Wm. Ellery Channing in Illinois in 1840.* Trans. Wis. Acad. Sci., Arts & Letters. 54:143-147.

_____, and K. Whitford. 1971. *Savanna in central Wisconsin USA.* Vegetatio 23:77-87.

Wisconsin Department of Natural Resources. 1968. Wisconsin Forest Resources Statistics, *North central survey report; Lake Michigan survey report; Lake Winnebego survey report; and Southeastern survey report.*

WSRS. 1970. *Wisconsin Agricultural Statistics.* Wisconsin Statistical Reporting Service, Madison. 70 p.

Wright, H. E. 1968. *The roles of pine and spruce in the forest history of Minnesota and adjacent areas.* Ecology 49:937-955.

_____, and D. G. Frey, (eds.). 1965. *The Quaternery of the United States.* Princeton Univ. Press, Princeton, N. J. 922 p.

Youngberg, C. T. 1951. *Evolution of prairie-forest soils under cover of invading northern hardwoods in the driftless area of southwestern Wisconsin.* Trans., Wisconsin Acad. Sci. 40:285-289.

Youse, L. 1901. *The plant ecology of Winona Lake.* Proc. Indiana Acad. Sci. pp. 192-204.

Zahner, R., and N. J. De Byle. 1965. *Effect of pruning the parent root on growth of aspen suckers.* Ecology 46:373-375.

ADDITIONAL REFERENCES

Benninghoff, W. S., and A. I. Gebben. 1960. *Phytosociological studies of some beech-maple stands in Michigan's Lower Peninsula.* Papers, Michigan Acad. Sci. 45:83-91.

Brown, R. T., and J. T. Curtis. 1952. *The upland conifer-hardwood forests of northern Wisconsin.* Ecol. Monogr. 22:217-234.

Cain, S. A. 1935. *Studies on virgin hardwood forest*: III. *Warren's Woods, a beech-maple climax forest in Berrien Co., Michigan.* Ecology 16:500-513.

Catenhusen, J. 1950. *Secondary successions on the peat lands of Glacial Lake, Wisconsin.* Trans., Wisconsin Acad. Sci. 40:29-48.

Christensen, E. M., J. J. Clausen, and J. T. Curtis. 1959. *Phytosociology of the lowland forests of northern Wisconsin.* Am. Midland Naturalist 62:232-247.

Cottman, G. S. 1930. *Indiana Dunes State Park: A history and description.* Indiana Dept. Conserv. Pub. 97.

Dansereau, P., and F. Segadas-Vianna. 1952. *Ecological study of the peat bogs of eastern North America.* Can. J. Bot. 30:490-520.

DenUyl, D. 1954. *Indiana's old growth forests.* Proc. Indiana Acad. Sci. 63:73-79.

Eyre, F. H., and R. K. LeBarron. 1944. *Management of jack pine stands in the Lake States.* USDA Tech. Bull. 863. 66 p.

Fowels, H. A. 1965 ed. *Silvics of forest trees of the United States.* USDA Forest Service, USDA Agr. Handbook 271. 762 p.

Fuller, G. D. 1912. *The cottonwood dune association.* Trans. Illinois Acad. Sci. 5:137-143.

_____. 1914. *Evaporation and soil moisture in relation to the succession of plant associations.* Bot. Gaz. 58:193-234.

_____. 1925. *The vegetation of the Chicago region: an outline of some of the principal plant associations together with lists of their principal species.* Univ. of Chicago Press, Chicago.

Gleason, H. A. 1910. *The vegetation of inland sand deposits of Illinois.* Bull. Ill. Lab. Nat. Hist. 9:23-174.

_____. 1917. *A prairie near Ann Arbor, Michigan.* Rhodora 19:163-165.

Graber, L. F., N. T. Nelson, W. A. Luekel, and W. B. Albert. 1927. *Organic food reserves in relation to the growth of alfalfa and other perennial herbaceous plants*. Wisconsin Agr. Exp. Sta. Res. Bull. 80.

Heath, M. E., D. S. Metcalfe, and R. E. Barnes, eds. 1973. *Forages, the science of grassland agriculture*. Iowa State Univ. Press, Ames. 755 p.

Hushen, T. W., R. O. Kapp, R. D. Bogue, and J. T. Worthington. 1966. *Presettlement forest patterns in Montcalm County, Michigan*. Mich. Bot. 5:192-211.

Jones, J. J. 1952. *A survey of fifteen forest stands in the early Wisconsin drift plain in Indiana*. Butler Univ. Bot. Stud. 10:182-204.

Keever, C. 1950. *Causes of succession on old fields of the Piedmont, North Carolina*. Ecol. Monogr. 20:229-250.

Laing, C. 1954. *The ecological life-history of the Ammophila breviligulata community on Lake Michigan dunes*. Ph.D. thesis. Univ. of Chicago.

Larsen, R. P. 1971. *Pear culture in Michigan*. Michigan State University Cooperative Extension Service. Extension Bull. E-519. East Lansing. 9 p.

Lee, M. B. 1945. *An ecological study of the floodplain forests along the White River system in Indiana*. Butler Univ. Bot. Stud. 7:155-165.

Livingston, B. E. 1903. *The relation of soils to natural vegetation in Roscommon and Crawford counties, Michigan*. Ann. Rep., Geol. Surv. Mich. pp. 1-30.

Parch, M. 1962. *Species distribution in a prairie in relation to water-holding capacity*. Proc., Minnesota Acad. Sci. 30:38-43.

Parmalee, G. W. 1953. *The oak upland community in southern Michigan*. Bull. Ecol. Soc. Amer. 34:84.

Peattie, D. C. 1930. *Flora of the Indiana dunes*. Field Museum of Nat. Hist., Chicago. 432 p.

Potzger, J. E. 1946. *Phytosociology of the primeval forest in central-northern Wisconsin and upper Michigan, and a brief post-glacial history of the lake forest formation*. Ecol. Monogr. 16:211-250.

Rhodes, J. W. 1933. *An ecological comparison of two Wisconsin peat bogs*. Milwaukee Public Museum Bull. 7:305-362.

Salisbury, E. J. 1925. *Note on the edaphic succession in some dune soils with special reference to the time factor*. J. Ecol. 13:322-328.

Stearns, F. W. 1951. *The composition of the sugar maple-hemlock-yellow birch association in northern Wisconsin*. Ecology 32:243-265.

Thomson, J. 1940. *Relic prairie areas in central Wisconsin*. Ecol. Monogr. 10:685-717.

Ward, R. T. 1954. *The beech forests of Wisconsin--changes in forest composition and the nature of the beech border.* Ecology 37:407-419.

Waterman, W. G. 1923. *Bogs of northern Illinois.* Trans. Illinois Acad. Sci. 16:214-225.

Whitford, H. N. 1901. *The genetic development of the forests of northern Michigan; a study in physiographic ecology.* Bot. Gaz. 31:289-325.

Wilson, L. R. 1939. *A temperature study of a Wisconsin peat bog.* Ecology 20:432-433.

Ward, D. V. 1974. Acclimatization responses of _Uca pugilax_ to sublethal concentrations of two insecticides. _Marine Biology_ 3:19-28.

Waterman, T. H. 1961. _Physiology of Crustacea_. Volume II. Academic Press. 681 pp.

Weiss, H. B. 1972. Population development of the _Uca_ crab population. _Maryland, a marine estuary species_. _Marine Biology_ ...

Wilson, K. A. 1989. Behavioral aspects of ... _Journal of ..._ 55:132-137.